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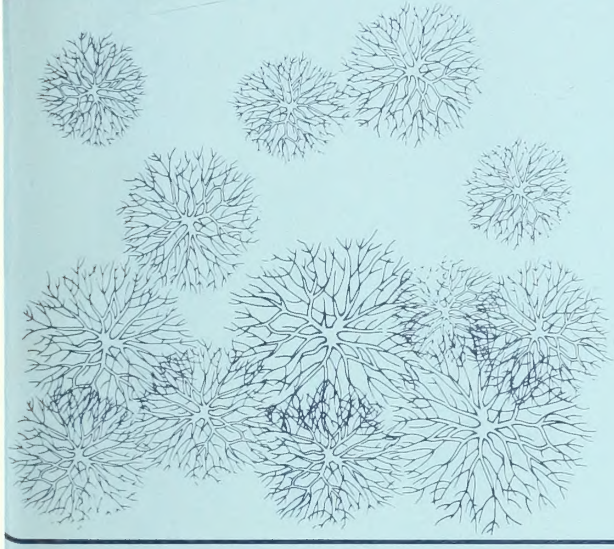

CONVERTING PARTIALLY-STOCKED ASPEN STANDS TO FULLY-STOCKED STANDS IN THE LAKE STATES: AN ECONOMIC ANALYSIS

Jeffrey T. Olson and Allen L. Lundgren

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Aspen
Birch
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North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture

PROGRAM REPORT

This paper is a contribution from the Aspen-Birch-Conifer Program. The Aspen-Birch-Conifer Program is a coordinated, multidisciplinary research effort. Its mission is to increase and integrate knowledge of the aspen-birch-conifer forests of the northern Great Lakes region in order to better identify and evaluate resource management alternatives.

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CONVERTING PARTIALLY-STOCKED ASPEN STANDS TO FULLY-STOCKED STANDS IN THE LAKE STATES: AN ECONOMIC ANALYSIS

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he 1968 Wisconsin Forest Survey (Spencer and rne 1972) shows large areas of aspen type[1] that not fully stocked. In terms of basal area stock- standards by Kittredge and Gevorkiantz 29), about 45 percent of the aspen type in Wis- sin is less than 50 percent stocked, and only 29 ent of the aspen type in Wisconsin is more 1 75 percent stocked. Future inventory vol- s of aspen in Wisconsin can be substantially eased by bringing understocked aspen stands ıll stocking.

tocking of future aspen stands can be increased ıspen lands by careful logging to insure all dual trees are felled or removed (Perala 1977). ases where competing shrubs and residual s are not removed during logging, the site t be prepared to insure regeneration of fully- ked stands of aspen suckers. Shearing is the t successful technique, but chainsaw felling, ling, and herbicide treatments are also recom- ıded. In certain cases prescribed burning may successful also. Such treatments will insure y-stocked aspen stands, but will require some estment.

n this paper we explore the feasibility of invest- ent to improve stocking of good site aspen on spen lands not currently fully stocked. Our ap- roach is to compare the expected future yield at ıarvest of fully-stocked to partially-stocked stands on similar sites. The discounted present value of the increase in future yield due to full stocking is an estimate of the amount that can be invested to achieve full stocking at the stated rate of return on the investment. Present values are estimated for both the immediate harvesting and regeneration of existing partially-stocked stands, and for delaying the harvest and regeneration.

ASSUMPTIONS

This analysis is based upon the following assumptions:

1. All stands in the aspen type are essentially pure aspen.
2. With logging and site preparation according to recommendations, formerly partially-stocked aspen stands will regenerate to fully-stocked stands and yields from future rotations will be comparable to the yields of present fully-stocked stands.
3. With logging but no site preparation, partially-stocked aspen stands will regenerate to partially-stocked stands and yields from future rotations will be comparable to existing partially-stocked stands.
4. Growth of aspen stands is dependent on the current age of the stand, and its present basal area, as given by Schlaegel's (1971) basal area growth equation.
5. To be operable for timber products, a stand must have an average diameter of at least 5.0 inches.

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[1] *Aspen type is defined as forests in which a mixture of quaking aspen* (Populus tremuloides), *bigtooth aspen* (populus grandidentata), *or balsam poplar* (Populus balsamifera), *singly, or in combination, comprise a plurality of the live tree stocking (Spencer and Thorne 1972).*

6. Only aspen site indices 60 through 80 will be considered, because Schlaegel's growth equation does not apply to lower sites.

ESTIMATING VOLUME YIELDS

Basal area (table 1) estimates reported by Kittredge and Gevorkiantz (1929) for fully-stocked, pure aspen stands were used as standards for determining the productivity potential of fully-stocked stands. The tables presented by Kittredge and Gevorkiantz are widely used to classify site productivity in the Lake States. They were used in our analysis as an optimistic estimate of potential basal area stocking in fully-stocked aspen stands.

Schlaegel's (1971) volume equations for aspen were used to determine stand volume from basal areas given by Kittredge and Gevorkiantz at various stand ages (table 1). The equations used are:

Table 1.—*Expected yields per acre of fully-stocked aspen*

Stand age	Height of dominants	Average d.b.h.	Stand basal area (ft²)	Total stem vol. (ft³)	Merch.[1] vol. (100 ft³)	E.V.I.[2] at discount rate r: 4	6	8	10
SITE INDEX 80									
20	46	3.3	88	1700	—	—	—	—	
25	53	4.0	99	2200	—	—	—	—	
30	59	4.8	110	2700	—	—	—	—	
35	65	5.6	120	3300	29	10.00	4.30	2.10	1.10
40	71	6.3	129	3800	36	9.50	3.90	1.70	.80
45	76	7.2	136	4300	41	8.50	3.20	1.30	.60
50	80	8.1	143	4800	46	7.50	2.60	1.00	.40
55	84	9.2	148	5200	51	6.70	2.20	.80	.30
60	87	10.3	153	5600	55	5.70	1.70	.60	.20
SITE INDEX 70									
20	40	2.9	83	1400	—	—	—	—	
25	46	3.8	92	1800	—	—	—	—	
30	51	4.2	102	2200	—	—	—	—	
35	57	4.8	111	2600	—	—	—	—	
40	62	5.4	120	3100	27	7.10	2.90	1.30	.60
45	67	6.2	127	3600	32	6.60	2.50	1.00	.50
50	70	7.0	133	3900	37	6.00	2.10	.80	.30
55	74	8.0	139	4300	41	5.40	1.70	.60	.20
60	76	9.0	144	4600	42	4.70	1.40	.50	.20
SITE INDEX 60									
20	34	2.5	76	1100	—	—	—	—	
25	39	3.0	86	1400	—	—	—	—	
30	44	3.5	94	1700	—	—	—	—	
35	48	4.0	103	2100	—	—	—	—	
40	53	4.5	110	2400	—	—	—	—	
45	57	5.2	117	2800	23	4.80	1.80	.70	.30
50	60	5.9	122	3100	28	4.60	1.60	.60	.20
55	63	6.7	128	3400	32	4.20	1.40	.50	.20
60	66	7.6	133	3700	36	3.90	1.20	.40	.10

[1] Merchantable volume includes all trees 3.6 inches d.b.h. and larger to a 3-inch top d.i.b. in stands 5.0 inches and larger.

[2] E.V.I. is the Expectation Value Index computed from the Equation $V_o = V_r \left[\frac{1}{(1+i)^t-1}\right]$ and is expressed in units of dollars per dollar of stumpage price per acre. These values may be used to estimate the optimal rotation age as shown above.

1. Total peeled volume (TV):

$$TV = 0.41898(BA)(HT) \qquad (1)$$

where:

BA=stand basal area in square feet/acre

HT=the height of dominant and codominant trees

TV=the total volume of the entire peeled stem in trees 0.5 inch d.b.h. and larger, expressed as cubic feet/acre.

Merchantable volumes in table 1 are to a 3-inch top and are determined by the following equation (Schlaegel 1971):

2. Merchantable volume (MV):

$$MV = (0.9858 - 5.4737(0.4876)^{DBH})(TV) \qquad (2)$$

where:

DBH=diameter outside bark at 4.5 feet above the ground for the tree of average basal area for all stems over 0.5 inch.

The Expectation Value Index (EVI) is an index of the present discounted value of all future incomes from the stand, assuming a stumpage price of $1 per unit of yield ouput (in this case, $1 per cunit of merchantable wood).[2] The present value of expected future stand yields is determined by multiplying the EVI by the stumpage price expected at the time of future harvest.

Rotation ages were selected for fully-stocked stands at the age where the EVI (table 1) was greatest. The EVI associated with fully-stocked stands managed on the selected rotations represents an index of the discounted value at a given interest rate, of an unending series of rotations from fully-stocked stands.

GROWTH OF PARTIALLY-STOCKED STANDS

Stands below rotation age may be harvested immediately, or they could be allowed to grow for a period of time until harvested at some rotation age. Thus, it is necessary to estimate both present yields and yields from delayed harvesting of existing partially-stocked stands.

Schlaegel's (1971) basal area growth function was used to estimate the basal area growth for a range of stand basal areas and ages. The equation is:

$$BAG = BA(5.3903 - \mathrm{Ln}BA)A^{-1} \qquad (3)$$

where:

BA=basal area of existing stand

A=stand age in years

Ln=natural logarithm

BAG=annual basal area growth

Schlaegel's basal area growth is not a function of site index, and thus implies that basal area growth is the same on all sites. Schlaegel's data, however, included only the better aspen sites, approximately site index 65 and higher. Kittredge and Gevorkiantz (1929) data indicate that on these higher sites, basal area growth rates do not differ markedly from one site to another. On poorer sites (site index 50 and below), however, the rate of basal area growth is substantially less. As a result, only sites 60 through 80 are considered.

Schlaegel's basal area growth equation was applied to site 70 stands to determine a percent of full stocking achieved at various ages by partially-stocked aspen stands. These percents of full stocking, table 2, were also applied to partially-stocked aspen stands on sites 60 and 80, since his equation

Table 2. Expected percent of full stocking achieved by delaying harvest of existing partially-stocked stands [1]

Current stand age	Current percent stocking	Harvest Age 25	30	35	40	45	50
		Percent					
20	25	36	45	51	57	61	65
	50	63	71	76	80	83	85
	75	87	93	96	98	99	100
30	25	—	—	31	37	42	46
	50	—	—	56	62	66	70
	75	—	—	80	84	87	89
40	25	—	—	—	—	30	34
	50	—	—	—	—	55	59
	75	—	—	—	—	78	81

[1] Based on Schlaegel's basal area growth projections on site index 70 lands.

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[2] *EVI is calculated as follows: Multiply the expected harvest yield by the appropriate discount rate multiplier for a perpetual series of periodic incomes for a specified stand age and discount rate. Lundgren (1966) presents a more detailed discussion.*

is independent of site. The results provide an estimate of basal area at the time of delayed harvest for partially-stocked stands. Applying these percentages to the merchantable yields from fully-stocked stands in table 1 gives expected yields of partially-stocked stands, shown in table 3.

Table 3. *Expected merchantable*[1] *volume yields in cunits per acre from partially-stocked aspen stands for a range of sites, ages, stocking percents, and rotations*

Existing stands age	Full stocking	Harvest Age 20	25	30	35	40	45	50
	Percent	*Hundreds of cubic feet*						
		Site Index 80						
20	25	—	—	—	14.8	20.5	25.0	29.9
	50	—	—	—	22.0	28.8	34.0	39.1
	75	—	—	—	27.8	35.3	40.6	46.0
30	25	—	—	—	9.0	13.3	17.2	21.2
	50	—	—	—	16.2	22.3	27.1	32.2
	75	—	—	—	23.2	30.2	35.7	40.9
40	25	—	—	—	—	9.0	12.3	15.6
	50	—	—	—	—	18.0	22.6	27.1
	75	—	—	—	—	27.0	32.0	37.3
		Site Index 70						
20	25	—	—	—	—	15.4	19.5	24.1
	50	—	—	—	—	21.6	26.6	31.4
	75	—	—	—	—	26.5	31.7	37.0
30	25	—	—	—	—	10.0	13.4	17.0
	50	—	—	—	—	16.7	2.1	25.9
	75	—	—	—	—	22.7	24.2	32.9
40	25	—	—	—	—	6.8	9.6	12.6
	50	—	—	—	—	13.5	17.6	21.9
	75	—	—	—	—	20.2	25.0	30.0
		Site Index 60						
20	25	—	—	—	—	—	14.0	18.2
	50	—	—	—	—	—	19.1	23.8
	75	—	—	—	—	—	22.8	28.0
30	25	—	—	—	—	—	9.7	12.9
	50	—	—	—	—	—	15.2	19.6
	75	—	—	—	—	—	20.0	24.9
40	25	—	—	—	—	—	6.9	9.5
	50	—	—	—	—	—	12.7	16.5
	75	—	—	—	—	—	17.9	22.7

[1] Stands are not considered merchantable until they reach an average d.b.h. of 5.0 inches and larger.

EVALUATION METHODS

Our analysis was designed to determine how much could be spent to achieve full stocking, rather than to estimate returns realized for an investment of some specified dollar amount. Cost of treatments required to improve stocking are available, but a great deal of variation is encountered when specific cases are reviewed. Stumpage prices also vary widely. Therefore, results are presented as discounted returns per acre, per dollar of stumpage price, at various discount rates. These are, in effect, the Expectation Value Index (EVI) (Lundgren 1966), and may be used in specific cases given the stumpage price per unit. Multiplying the EVI by the stumpage price per unit gives the gross return per acre. Net returns may then be determined by subtracting the discounted costs from the gross discounted returns. The units of output presented are cunits (100 ft^3 of solid wood). Since a cunit represents approximately 25 percent more wood than a cord, the price per cunit is approximately 25 percent greater than the price per cord.

RESULTS

Table 4 presents the margin for investment index (MII) for converting partially-stocked aspen stands to fully-stocked aspen stands. Economic rotation ages are shown for both fully- and partially-stocked stands. The column "MII" presents the difference between the expectation value index for an infinite series of economic rotations of fully-stocked stands, and an infinite series of economic rotations of partially-stocked stands, on similar sites. Economic rotations were selected at the age at which the EVI was highest. Margin for investment indexes were determined for a range of discount rates from 4 to 10 percent.

The margin for investment represents an *index* of the maximum that could be spent to convert partially-stocked aspen stands to full stocking and still realize some specified rate of return. The actual breakeven dollar amount that could be invested to achieve full stocking can be estimated by multiplying the column labeled "MII" by the expected stumpage price. The highest potentials for investment are shown by poorly-stocked, older age stands. Table 4 shows that if costs are the same the best conversion opportunities exist on site index

Table 4. *The Margin for Investment Index (MII)*[1] *for converting partially-stocked aspen stands to full stocking for various sites, stand descriptions, and discount rates*

Site Index 80

Initial stand age	Discount rate	Initial stocking[2] (25 percent) Rotation age Partially-stocked	Fully stocked	MII	Initial stocking 50 percent Rotation age Partially-stocked	Fully stocked	MII	Initial stocking 75 percent Rotation age Partially-stocked	Fully stocked	MII
20	4	40	35	4.60	40	35	2.40	35	35	.60
	6	35	35	2.10	35	35	1.00	35	35	.10
	8	35	35	1.00	35	35	.50	35	35	.10
	10	35	35	.60	35	35	.30	35	35	.10
30	4	45	35	6.40	40	35	4.10	40	35	2.10
	6	40	35	2.90	35	35	1.90	35	35	.80
	8	35	35	1.40	35	35	.90	35	35	.40
	10	35	35	.80	35	35	.50	35	35	.20
40	4	50	35	7.40	40	35	5.30	40	35	2.90
	6	40	35	3.30	40	35	2.40	40	35	1.40
	8	40	35	1.70	40	35	1.20	40	35	.80
	10	40	35	.90	40	35	.70	40	35	.50
Site Index 70										
20	4	40	40	3.10	40	40	1.40	40	40	.10
	6	40	40	1.20	40	40	.60	40	40	.10
	8	40	40	.60	40	40	.30	40	40	.00
	10	40	40	.20	40	40	.10	40	40	.00
30	4	50	40	4.30	40	40	2.70	40	40	1.10
	6	40	40	1.80	40	40	1.10	40	40	.50
	8	40	40	.80	40	40	.50	40	40	.20
	10	40	40	.40	40	40	.20	40	40	.10
40	4	50	40	5.00	45	40	3.50	40	40	1.80
	6	45	40	2.20	40	40	1.50	40	40	.70
	8	40	40	1.00	40	40	.70	40	40	.30
	10	40	40	.40	40	40	.30	40	40	.10
Site Index 60										
20	4	50	45	1.80	45	45	.80	45	45	.10
	6	45	45	.70	45	45	.30	45	45	.00
	8	45	45	.20	45	45	.10	45	45	.00
	10	45	45	.10	45	45	.00	45	45	.00
30	4	50	45	2.70	50	45	1.60	45	45	.70
	6	45	45	1.00	45	45	.60	45	45	.20
	8	45	45	.40	45	45	.20	45	45	.10
	10	45	45	.20	45	45	.10	45	45	.00
40	4	50	45	3.20	50	45	2.10	50	45	1.10
	6	50	45	1.20	45	45	.80	45	45	.40
	8	45	45	.50	45	45	.30	45	45	.10
	10	45	45	.20	45	45	.10	45	45	.10

[1] MII is found by subtracting the E.V.I. for partially-stocked stands from the E.V.I. of fully-stocked stands on the same site, and is expressed as dollars per acre per dollar of stumpage price for a cunit of timber.

[2] Stands are described in terms of the percent of full stocking they have achieved at the specified age.

80 stands that have only 25 percent of full stocking at age 40. The next best opportunity exists on site 80, age 30, 25 percent stocked stands, followed by stands 50 percent of full stocking at age 40, and lastly, stands 25 percent of full stocking at age 20. The other sites also follow the same pattern.

DELAY OF HARVEST OF PARTIALLY-STOCKED STANDS BEFORE INVESTMENT TO ACHIEVE FULL STOCKING

Presumably, the landowner (based on table 4) would be willing to convert partially-stocked stands to full stocking at any time that the cost of conversion was less than the margin for investment. The landowner would be indifferent towards conversion opportunities where the margin for investment was equal to the cost of conversion, and would not undertake those projects where conversion costs exceed the margin available. For example, if the landowner expected a 4 percent rate of return on his investments and had an aspen stand that had achieved 25 percent of full stocking by age 30 on site index 80 lands, his available margin for investment is \$6.40 per dollar of stumpage price, per acre (table 4). If the stumpage price for aspen were \$4.50 per cunit, the landowner could invest up to \$28.80 per acre to convert his partially-stocked stands to full stocking. If his conversion costs were higher than \$28.80 per acre, he would not earn his desired 4 percent rate of return; if less, he would earn at *least* his desired 4 percent return.

The difference between the margin for investment at a given interest rate and the cost of conversion is the net present value of the returns the landowner would receive from conversion (NPVC). Where the net present value is positive, partially-stocked stands should be converted to full stocking at the point in time where the present value of the existing partially-stocked stand plus the net present value of conversion is maximized at a specified rate of interest. This occurs when the rate of increase in the net value of the existing stand plus conversion falls below the desired interest rate.

Mathematically, the rule is given by the following equation:

Harvest in year t when:

$$\frac{\text{FVPS} + \text{NPVC}}{\text{PVPS} + \text{NPVC}} = (1+r)^t \qquad (4)$$

where:

PVPS = Present value of existing partially-stocked stand
= Present yield volume × stumpage price (from table 3)

FVPS = Future value of existing partially-stocked stand in t years
= Future yield volume x stumpage price (from table 3)

NPVC = Net present value of conversion to fully-stocked stands
= EVI_{FS} × stumpage price – conversion cost (from table 1)

r = interest rate desired

This equation is the future value of the yield of an existing partially-stocked stand grown for t years and then harvested, plus the net value of the site for production of an infinite rotation of fully-stocked stands, divided by the present value of the existing partially-stocked stand if harvested today plus the net value of the site. When the ratio is equal to, or falls below the interest rate, r, the present value has been maximized and the stand should be harvested. As an example, consider the case of an aspen site index 80 stand that has reached 25 percent of full stocking by age 30. The tabulation below shows yields in cunits per acre that would be expected:

Stand age	*Merchantable volume* [3]cunits/acre
30	0
35	9.0
40	13.3
45	17.2
50	21.2

Assume also the following:

1. stumpage price . . . \$4.50/cunit (constant relative to inflation)
2. Conversion cost . . . \$25.00/acre (constant relative to inflation)
3. desired rate of return . . . 4 percent

Solving equation (4) is a stepwise process as follows:

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[3] *Source: Table 3.*

Step 1: Check rate of value growth from stand age 30 to 35 years

The yield volume from this 30-year-old partially-stocked stand is 0 cunits (table 3). Thus:

$PVPS = 0 \times \$4.50/cunit = 0$

The yield volume from this stand when it is 35 years old will be 9.0 cunits. Thus:

$FVPS = 9.0 \text{ cunits} \times \$4.50/cunit = \$40.50$

The expectation value index for a fully-stocked stand on this site with a 4 percent discount rate and a rotation age of 35 years is 10.00.

Thus:

$NPVC = 10.00 \text{ cunits} \times \$4.50/cunit - \$25.00 = \$20.00$

Putting this together:

$$(1+r)^5 = \frac{\$40.50+\$20.00}{0+\$20.00} = 3.025$$

$$r = 24.8 \text{ percent}$$

Obviously, the annual rate of increase in value by delaying harvest of the existing partially-stocked stand is higher than the desired 4 percent rate of return. The decision would be to delay harvest and conversion for at least 5 years.

Step 2: Check rate of value growth from stand age 35 to 40 years.

Repeating the procedure outlined above, the anticipated value growth of delaying harvest from 35 to 40 years is 1.32, an annual rate of 5.7 percent. This exceeds the alternative rate of value growth, so the stand should not be harvested at age 35.

Step 3: Check value growth from stand age 40 to 45.

Value growth of delaying harvest from age 40 to 45 is 1.22, just slightly above the desired rate. The owner could harvest the stand at age 40, or wait until age 45 when the anticipated value growth will fall below the desired 4 percent rate of return.

In this example, the landowner would hold his existing partially-stocked stand until it is 45 years old (15 additional years) before harvesting and converting the stand to full stocking. Summarizing the analysis in step 1, he found that the rate of value growth from stand age 30 to stand age 35 exceeded his desired rate of return, and he determined to hold it at least until it was 35 years old. In step 2, he found that the rate of value growth from stand age 35 to stand age 40 was still in excess of his 4 percent alternative rate of return, and he again determined to hold the stand. In step 3, the landowner found that the rate of value increase from stand age 40 to stand age 45 was just equal to his desired rate of return. He therefore determined to hold his partially-stocked aspen stand 15 years until it reached a stand age of 45 years, at which time he will invest in silvicultural treatments to insure that future stands will be fully stocked.

CONCLUSIONS

This analysis presents a methodology useful in making a quick estimate of the economic potential for conversion of partially-stocked aspen stands to full stocking. Expectation value indices allow application of the results of this paper to local areas where stumpage prices and treatment costs are known. The margin available for investment when converting partially-stocked aspen stands to full stocking is small, especially at higher interest rates and on lower sites. Conversion opportunities are best for poorly-stocked older stands, since their yields at economic maturity are much less than the yield of fully-stocked stands. Poorly-stocked young stands will tend to approach the yield of fully-stocked stands over time, and at economic maturity their yields will more closely approximate the yields of fully-stocked stands on the same sites.

Where converted to full stocking, existing partially-stocked stands should be harvested when the present value of the stand plus the net value from conversion is maximized. This paper presents a means of estimating when this value will be maximized. The method is based on the rate of value growth when harvesting is delayed for a given period. The time of delayed harvest will vary depending upon stumpage price, interest rate, and the profit realized from converting partially-stocked stands.

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Shhhh...noise pollutes, too!

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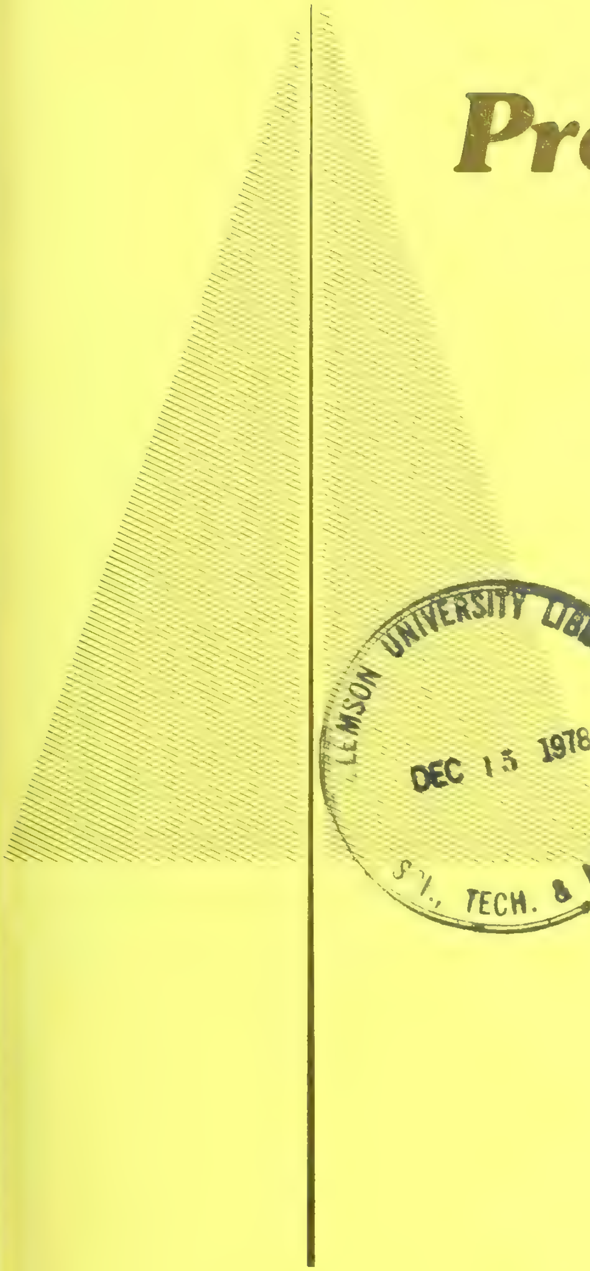

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1977
MIDWEST FOREST MENSURATIONISTS Meeting

North Central Forest Experiment Station
Forest Service, U.S. Department of Agriculture

The Midwest Mensurationists are a group of scientists working on quantitative problems in forestry in the mid-section of the country. They meet periodically and informally to discuss matters of mutual interest. The papers included here were presented at their 1977 meeting in Lutsen, Minnesota.

North Central Forest Experiment Station
John H. Ohman, Director
Forest Service - U.S. Department of Agriculture
1992 Folwell Avenue
St. Paul, Minnesota 55108

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ERRORS IN SAMPLING PLANS BASED ON WALD'S SEQUENTIAL PROBABILITY RATIO TEST

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School of Natural Resources, University of Michigan,
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Various sequential sampling plans based on Wald's Sequential Probability Ratio Test (SPRT) (Wald 1947, Wetherill 1966) have been developed for sampling forest populations. Such plans have been used to test hypotheses for decisionmaking and to classify populations. At least 27 plans have been developed to aid in monitoring insect populations or their damage.

Some plans were based on one SPRT to yield a two decision procedure such as control versus no control, while others were based on two SPRT's to yield a three decision procedure such as light versus medium versus heavy infestations. Because most sequential sampling plans in forestry have been applied to the field of entomology, this paper will emphasize entomological examples.

The sample size needed to make a decision to accept or reject a hypothesis for sequential sampling plans based on Wald's SPRT is a random variable. A decision to accept or reject a hypothesis or to continue sampling is made after each observation is taken, and observations are taken until enough evidence has been collected to make one of the terminating decisions. Such plans usually require only 40 to 60 percent as many observations as an equally reliable fixed sample size procedure. They are intuitively appealing in that few observations are needed to make a terminating decision when, for example, insect populations are sparse or abundant. Given the budget restraints faced today, sequential sampling plans should find wide applicability where we need to classify populations or compare populations with some standard for decisionmaking purposes and observations are time consuming, costly, and/or destructive. Such plans would also be useful when it is important to make a quick decision.

The first step in constructing a sequential sampling plan is to define the sampling unit and associated random variable of interest. The distribution of the random variable must then be determined. All of the plans developed to sample forest populations are based on either the binomial, negative binomial, normal, or Poisson distributions. For the normal and negative binomial distributions, the population variance σ^2 and the clumping parameter K, respectively, are assumed known, and if unknown must be estimated.

The second step is to set the class limits (e.g., economic thresholds or pest density levels), the simple null and alternative hypothesis parameter values of the underlying random variable, and the associated risk levels (probabilities of a Type I Error (α) and a Type II Error (β)). The gap between the two class limits (the interval between treatment and nontreatment thresholds) depends on the biology and behavior of the insect and its damage (Knight 1967; Waters 1955, 1974). The two class limits define three decision zones: the two terminating decisions or category classifications such as no control (acceptance of the null hypothesis) and control (acceptance of the alternative hypothesis), and the no decision zone (continue sampling).

Because there are two class limits or simple hypotheses that are used to construct a SPRT, two types of error can occur in decisionmaking:

(1) accepting the null hypothesis when the alternative hypothesis is true and (2) accepting the alternative hypothesis when the null hypothesis is true. The probabilities (risks) of these errors must be set in advance according to the seriousness of each error.

After the decision boundaries for a given SPRT have been developed given the underlying distribution and the class limits and associated risks, the operating characteristic (OC) and average sample number (ASN) properties of the test should be determined. Wald (1947) has developed OC and ASN equations to describe the properties of the test for all possible values of the random variable of interest. The OC equation or curve shows the probability of accepting the null hypothesis or lower classification, and the ASN equation or curve shows the average number of observations needed to make a terminating decision. The shapes of the OC and ASN curves depend upon the underlying distribution and class limits and associated risks (Waters 1974, Onsager 1976).

In all of the sequential sampling plans developed to sample forest populations, it is assumed that Wald's OC and ASN equations describe the actual OC and ASN functions of the plan, which means that the nominal values used to construct a SPRT are assumed to be the actual values. Wald's equations are developed on the assumption that a terminating decision is made as soon as a decision boundary is crossed. This assumption is not true because of the integer nature of the decision process of a SPRT, which results in overshooting of the decision boundaries when a terminating decision is made (fig. 1) (Wald 1947). Thus, Wald's equations are not accurate.

Wald's equations also assume that (1) only one observation is taken at each stage of the sequential process, (2) terminating decisions are possible after one observation has been taken, and (3) there is no upper limit to the number of observations taken before a terminating decision is made. Many forest researchers have modified the decision process of the SPRT by taking more than one observation at each stage of the sampling plan, not making a terminating decision until some minimum number of observations has been taken, and forcing a terminating decision to be made at some maximum number of observations. Any of these modifications will, of course affect the actual OC and ASN functions of sampling plan. However, in all application where one or more of these modifications ar made, Wald's OC and ASN equations are stil used to describe the properties of the samplin plan.

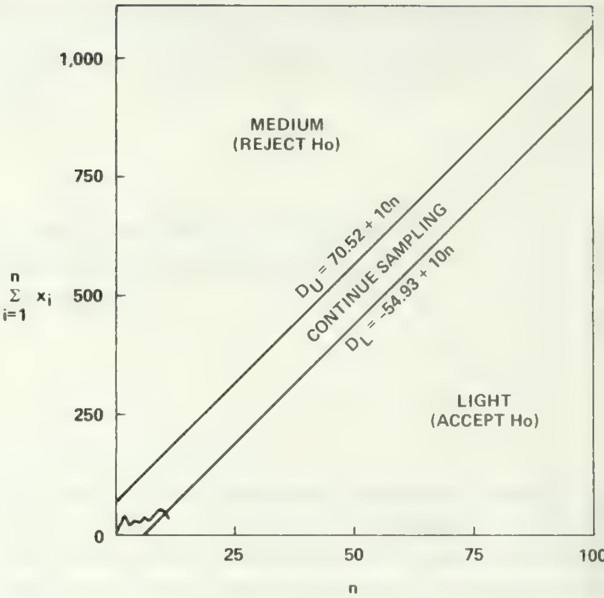

Figure 1. — *Acceptance (d_L) and rejection (d_U decision boundaries for the lodgepole needle miner sequential sampling plan. Lines con necting points (.) show a sequential sample o 11 observations yielding a decision of light infestation. Notice overshooting of the lowe decision boundary.*

This paper examines (1) the errors inherent i Wald's OC and ASN equations due to overshoot ing of the decision boundaries and (2) the effect of the above modifications on the accuracy c Wald's equations for sequential sampling plan based on the normal distribution using Mont Carlo procedures.

WALD'S SPRT — NORMAL DISTRIBUTION

In forest sampling, Wald's SPRT is used t test the simple null hypothesis $H_0 : \theta = \theta_0$ agains the simple alternative hypothesis $H_1: \theta = \theta_1$ ($\theta_1 > \theta_0$), where θ is the test parameter of the distribution of the random variable X. The binomial distribution is used to describe X when X takes on one of two values ($X = 1$ for tree or plant or part of tree or plant infested and $X = 0$ for tree or plant or part of tree or plant not infested). The negative binomial, normal, or Poisson distributions are usually used to describe X when X is the number of insects per sampling unit. θ_0 and θ_1 define the class limits for the two decision categories — control or no control. The probability of a Type I Error (α) is the probability of rejecting H_0 when $\theta = \theta_0$, and the probability of a Type II Error (β) is the probability of rejecting H_1 when $\theta = \theta_1$. At the class limits, θ_0 and θ_1, the risk levels are set according to the seriousness of the two errors.

The two above simple hypotheses are used to develop the following decision rule: $H_0: \theta \leq \theta_0$ (no control) versus $H_1: \theta > \theta_0$ (control). The class limits, θ_0 and θ_1, are critical values of θ. If $\theta \geq \theta_1$ (the zone of rejection), protect against accepting H_0 by setting β at θ_1. If $\theta \leq \theta_0$ (the zone of acceptance), protect against rejecting H_0 by setting α at θ_0. If $\theta_0 < \theta < \theta_1$ (the zone of indifference), it does not matter what decision is made if θ is about halfway between θ_0 and θ_1 but becomes more important what decision is made as $\theta \rightarrow \theta_0$ and $\theta \rightarrow \theta_1$. This concern is expressed by the values of α and β set at θ_0 and θ_1, respectively. The values θ_0, θ_1, α, and β given the distribution of X describe a particular SPRT.

Decision Boundaries

The SPRT bases its decisons on a sequence of observations ($x_1, x_2, \ldots$) from the given distribution of the random variable X. At each stage of the test, an observation is taken at random from the given distribution $f(x,\theta)$, and the probability ratio

$$R_n = \prod_{i=1}^{n} [\, f(x_i,\theta_1)/f(x_i,\theta_0)\,],$$

based on n observations taken up to and including the n^{th} stage is calculated. At each stage one of the following decisions is made:

(1) If $R_n \geq A$, stop sampling and reject H_0.
(2) If $R_n \leq B$, stop sampling and accept H_0.
(3) If $B < R_n < A$, continue sampling.

$A \simeq (1-\beta)/\alpha$ and $B \simeq \beta/(1-\alpha)$. The approximate equalities are due to the fact that the number of observations is a discrete integer variable that causes overshooting of the decision boundaries before a terminating decision can be made for a SPRT (fig. 1). Observations are taken until one of the terminating decisions is made.

R_n can be simplified by taking the natural logarithm of each density function ratio in the product R_n, which yields $Z_n = \sum_{i=1}^{n} Z_i$ where $Z_i = \ln [\, f(x_i,\theta_1)/f(x_i,\theta_0)]$. The decision procedure is now

(1) If $Z_n \geq a$, stop sampling and reject H_0.
(2) If $Z_n \leq b$, stop sampling and accept H_0.
(3) If $b < Z_n < a$, continue sampling.

$a \simeq \ln A$ and $b \simeq \ln B$.

Z_n is usually converted to the statistic $\sum_{i=1}^{n} x_i$, which is easier to calculate, by setting $Z_n = a$ and $Z_n = b$ and solving for $\sum_{i=1}^{n} x_i$ to determine the upper rejection ($D_U = \sum_{i=1}^{n} x_i = h_2 + sn$) and lower acceptance ($D_L = \sum_{i=1}^{n} x_i = h_1 + sn$) boundaries, respectively. The decision boundaries are parallel straight lines with intercepts h_1 and h_2 and common slopes. The decision is now:

(1) If $\sum_{i=1}^{n} x_i \geq h_2 + sn$, stop sampling and reject H_0.
(2) If $\sum_{i=1}^{n} x_i \leq h_1 + sn$, stop sampling and accept H_0.
(3) If $h_1 + sn < \sum_{i=1}^{n} x_i < h_2 + sn$, continue sampling.

h_1, h_2, and s are calculated from θ_0, θ_1, α, and β. For the normal distribution,

$$f(x) = \frac{1}{(2\pi)^{1/2}\sigma} e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

$$h_1 = \frac{b\sigma^2}{\mu_1 - \mu_0}$$

$$h_2 = \frac{a\sigma^2}{\mu_1 - \mu_0}$$

$$s = \frac{\mu_1 + \mu_0}{2}$$

when the test parameter $\theta = \mu$, the mean of the distribution and the nontest parameter σ^2 is the variance of the distribution.

Once the density function f(x), θ_0, θ_1, α, and β are determined, the decision boundaries D_U and D_L are easily obtained from the probability ratio R_n. For the normal distribution, σ^2 is assumed known and if unknown must be estimated. Even though the decision boundaries are parallel straight lines, the probability of making a terminating decision is one. The class limits used for decisionmaking are in terms of the mean of the underlying distribution and are functions of the test parameter θ. For the normal distribution, the test parameter μ is the mean of the distribution. The equations for h_1, h_2, and s were summarized by Waters (1955) for the binomial, negative binomial, normal, and Poisson distributions. Talerico and Chapman (1970) developed a Fortran IV computer program (SEQUAN) to calculate h_1, h_2, and s and plot the decision boundaries for the four distributions above.

A sequential sampling plan based on the normal distribution will be used as an example throughout this paper. Stark (1952) developed a plan for classifying lodgepole needleminer (*Recurvaria milleri* Busck.) populations as light, medium, or heavy to make preliminary surveys of needleminer outbreak areas. The sampling unit was a branch tip including needles up to 5 years old, and the random variable was the number of live larvae per branch tip. It was determined that the number of live larvae per branch tip followed approximately a normal distribution, and the standard deviation σ was estimated to be 15.62. One of the SPRT's in the three decision (2SPRT) procedure was used to test whether insect infestations were light or medium. The class limits μ_0 and μ_1 were set at 5 and 15 larvae per branch tip, respectively, and α and β were set at 0.05 and 0.10, respectively.

The decision rule was to classify an infestation as light if $\mu \le \mu_0 = 5$ and to classify it as heavy if $\mu > \mu_0 = 5$. If $\mu = 5$ for a specific needleminer population, the SPRT would indicate a medium infestation 1 out of 20 times when the infestation was light. If $\mu = 15$ for a specific needleminer population, the SPRT would indicate a light infestation 1 out of 10 times when the infestation was medium. Using the formulas for the normal distribution, h_1, h_2, and s were calculated to be -54.93, 70.52, and 10, respectively (fig. 1).

Wald's OC and ASN Equations

The OC function $L(\theta)$ is the probability of ac cepting H_0 as a function of θ. Wald's OC equa tion is $L(\theta) \simeq (A^{h(\theta)}-1)/A^{h(\theta)}-B^{h(\theta)})$ where and B are as defined earlier and $h(\theta)$ is such tha

$$\int_{-\infty}^{\infty} \frac{f(x,\theta_1)}{f(x,\theta_0)}^{h(\theta)} f(x,\theta)dx = 1$$

$$\sum_{x} \frac{f(x,\theta_1)}{f(x,\theta_0)}^{h(\theta)}$$

where x is a continuous or discrete variable, re spectively, and $h(\theta) \neq 0$ (Wald 1947). To obtai points on the OC function, one of the above equa tions is solved for $h(\theta)$, θ is determined for var ous values of $h(\theta)$, and $L(\theta)$ is calculated. Whe $h(\theta) = 1$ and -1, $\theta = \theta_0$ and θ_1, respectively. F the case where $h(\theta) = 0$, $L(\theta) \simeq a/(a-b)$ (Wal 1947). For the normal distribution,

$$L(\mu) \simeq (A^{h(\mu)}-1)/(A^{h(\mu)}-B^{h(\mu)})$$

$$h(\mu) = \frac{\mu_1 - \mu_0 - 2\mu}{\mu_1 - \mu_0}$$

where $\theta = \mu$.

The ASN function $E_\theta(n)$ is the average num ber of observations needed to make a terminat ing decision. Wald's ASN equation is

$$E_\theta(n) \simeq E_\theta(Z_n)/E_\theta(Z) \text{ for } h(\theta) \neq 0$$

where $Z_n = \sum_{i=1}^{n} Z_i$ as defined earlier, $E_\theta(n) \simeq b$ (θ) + a[1-L(θ)], and $E_\theta(Z) = E_\theta[\ln(f(x,\theta_1)$ $f(x,\theta_0))]$ (Wald 1947). To obtain points on th ASN function, $E_\theta(n)$ is calculated for severa values of θ determined from $h(\theta)$ above. For th case where $h(\theta) = 0$, $E_\theta(n) \simeq ab/E_\theta(Z^2)$ (Wald 1947). For the normal distribution,

$$E_\mu(n) \simeq bL(\mu) + a[1-L(\mu)]$$

$$E_\mu(Z) = \left(\frac{\mu_1 - \mu_0}{\sigma^2}\right)\left(\mu - \frac{\mu_1 - \mu_0}{2}\right)$$

$$E_\mu(Z)^2 = \frac{(\mu_1 - \mu_0)^2}{\sigma^2}$$

OC and ASN points for $h(\theta) = 4(-0.5)-4$ will usually describe the OC and ASN functions adequately. Formulas for Wald's OC and ASN equations for the four distributions discussed earlier were summarized by Waters (1955). Talerico and Chapman (1970) and I have developed Fortran IV computer programs to calculate OC and ASN points for selected values of $h(\theta)$. My program also calculates Monte Carlo $\widehat{OC}$ and $\widehat{ASN}$ points for selected values of $h(\theta)$. Wald's OC and ASN points for various values of $h(\mu)$ and μ are given in table 1 for the sampling plan presented earlier to classify populations of the lodgepole needleminer, and the resulting OC and ASN equations are shown in figure 2.

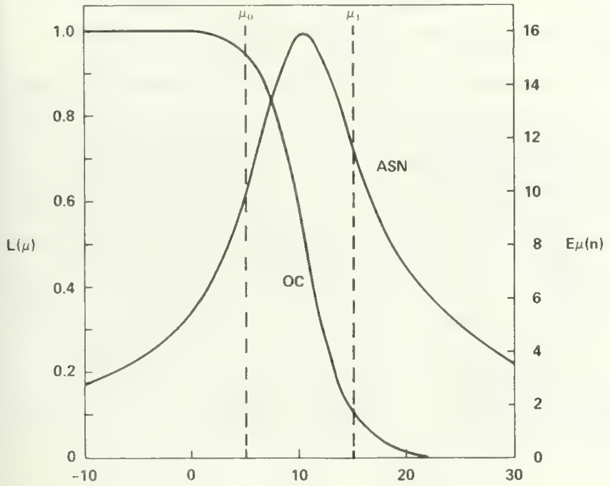

Figure 2. — *Wald's approximate OC ($L(\mu)$) and ASN ($E_\mu(n)$) functions for the lodgepole needleminer sequential sampling plan. Notice that $L(\mu) = 1 - \alpha = 0.95$ at $\mu = \mu_0 = 5$ and $L(\mu) = \beta = 0.10$ at $\mu = \mu_1 = 15$.*

As mentioned earlier, Wald's OC and ASN equations, and associated nominal α and β, are only approximate in that they are based on the assumption that a terminating decision is made as soon as one of the decision boundaries is crossed. Because the number of observations is a discrete integer variable, overshooting of a decision boundary almost always occurs before a terminating decision is made. Wald (1947) states that the errors inherent in his equations due to overshooting are small if α and β are small (less than 0.05) and the class limits θ_0 and θ_1 are sufficiently close together. Because α and β are usually 0.10 (0.05 at the smallest) and the class limits are wide for most sampling plans in forestry, Wald's equations may not be good approximations to the unknown actual OC and ASN functions.

Sequential sampling plans require substantially fewer observations than equally-reliable fixed sample size procedures. For the lodgepole needleminer example, where $\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$, approximately 21 observations are needed to yield $\alpha = 0.05$ @$\mu_0 = 5$ and $\beta = 0.10$ @$\mu_1 = 15$ for a fixed sample size Ƶ - test. Compare this sample size with the ASN function for the sequential sampling plan (fig. 2). The advantage of the sequential sampling plan is clear. However, in comparing the two procedures, it must be remembered that Wald's equations are only approximate.

Table 1. — *Wald's Operating Characteristic ($L(\mu)$) and Average Sample Number ($E_\mu(n)$) points for several values of $h(\mu)$ and μ for the lodgepole needleminer sequential sampling plan*

h(μ)	μ	L(μ)	$E_\mu(n)$	h(μ)	μ	L(μ)	$E_\mu(n)$
4	-10	1.000	2.75	-0.25	11.25	0.405	15.76
3	- 5	1.000	3.66	- .5	12.5	0.268	14.73
2	0	0.997	5.45	-1	15	0.100	11.60
1	5	0.950	9.73	-2	20	0.011	6.91
0.5	7.5	0.828	13.32	-3	25	0.001	4.69
0.25	8.75	0.711	14.96	-4	30	0.000	3.53
0	10	0.562	15.88				

THE ERRORS IN WALD'S OC AND ASN EQUATIONS

To investigate the effects of overshooting the decision boundaries of a given sequential sampling plan on the accuracy of Wald's OC and ASN equations, Monte Carlo simulation techniques were used to estimate the unknown actual OC and ASN functions. A distribution generator was developed to simulate taking observations at random from a normal distribution. The errors in Wald's equations were examined by comparing:

(1) Wald's nominal risk values (α and β) and associated average sample numbers (ASN) with Monte Carlo estimates of the actual risk values ($\hat{\alpha}$ and $\hat{\beta}$) and associated average sample numbers ($\hat{\text{ASN}}$) at class limits $\mu_0[\,h(\mu) = 1]$ and $\mu_1[\,h(\mu) = -1]$ for various values of $\alpha = \beta$ and μ_0 and μ_1; and (2) Wald's OC and ASN equations and Monte Carlo estimates of the unknown actual OC and ASN functions for the lodgepole needleminer example.

A sensitivity analysis indicated that 5,000 an 1,000 samples from a normal distribution (trial or iterations) yielded adequate accuracy for th Monte Carlo $\hat{\text{OC}}$ and $\hat{\text{ASN}}$ values at $h(\mu) = \pm$ and $h(\mu) \neq \pm 1$, respectively. Unless otherwis stated, that many iterations were used. Any de sired degree of accuracy can be obtained but th cost increases with the number of iterations Throughout the discussion, OC and ASN refer t Wald's equations, $\hat{\text{OC}}$ and $\hat{\text{ASN}}$ refer to Mont Carlo functions, $\text{SD}_{\hat{OC}} = [\,\hat{\text{OC}}(1-\hat{\text{OC}})/\#\text{trials-}1]^{1/2}$ is the standard deviation of the $\hat{\text{OC}}$ value $\text{SE}_{\hat{ASN}}$ is the standard error of the $\hat{\text{ASN}}$ value and $\text{RE}_{ASN} = (\text{ASN}-\hat{\text{ASN}})/\hat{\text{ASN}}$ is th estimated error of Wald's ASN value.

The Pattern of Errors

To establish if there are any trends in the errors inherent in Wald's equations, Wald an Monte Carlo OC and ASN values at $h(\mu) = \pm$ were compared for $\alpha = \beta = 0.05$, 0.10, and 0.2 and $\delta_1 = 0.1$, 0.25, 0.5, 1, 2, and 3 (tables 2 an 3). $\delta_1 = (\mu_1 - \mu_0)/\sigma$ is the noncentrality para meter of the standardized normal distributior

Table 2. — *Comparison of Wald's and Monte Carlo values of α and β at $h(\mu) = \pm 1$ for several values of δ_1 and $\alpha = \beta$ for the normal distribution*

δ_1	$\alpha = \beta$								
	0.05			0.10			0.20		
	$\hat{\alpha}$	$\text{SD}_{\hat{\alpha}}$	RE_{α}	$\hat{\alpha}$	$\text{SD}_{\hat{\alpha}}$	RE_{α}	$\hat{\alpha}$	$\text{SD}_{\hat{\alpha}}$	RE_{α}
0.1	0.047	0.0015	0.064	0.093	0.0021	0.075	0.192	0.0020	0.042
.25	.046	.0010	.087	.088	.0014	.136	.177	.0019	.130
.5	.037	.0009	.351	.077	.0013	.299	.156	.0018	.282
1	.028	.0008	.786	.057	.0012	.915	.123	.0016	.626
2	.016	.0006	2.12	.031	.0009	2.23	.064	.0012	2.12
3	.008	.0004	5.25	.016	.0006	5.25	.028	.0008	6.14

Table 3. — *Comparison of Wald's and Monte Carlo values of Average Sample Number (ASN) at $h(\mu) = \pm 1$ for several values of δ_1* and *$\alpha = \beta$ for the normal distribution*

δ_1	$\alpha = \beta$											
	0.05				0.10				0.20			
	ASN	$\hat{\text{ASN}}$	$\text{SE}_{\hat{ASN}}$	RE_{ASN}	ASN	$\hat{\text{ASN}}$	$\text{SE}_{\hat{ASN}}$	RE_{ASN}	ASN	$\hat{\text{ASN}}$	$\text{SE}_{\hat{ASN}}$	RE_{ASN}
0.1	530.0	541.5	3.87	-0.021	351.6	367.5	1.97	-0.043	166.4	179.1	0.71	-0.074
.25	84.8	90.9	.32	- .067	56.2	62.2	.23	- .096	26.6	31.8	.12	- .164
.5	21.2	24.2	.08	- .124	14.1	17.1	.06	- .175	6.6	9.5	.04	- .305
1	5.3	7.0	.023	- .243	3.5	5.2	.018	- .327	1.7	3.2	.012	- .469
2	1.3	2.3	.007	- .435	.9	1.9	.006	- .526	.4	1.5	.004	- .733
3	.6	1.4	.003	- .571	.4	1.2	.003	- .667	.2	1.1	.002	- .818

The OC value at $h(\mu) = 1$ is $1-\alpha$, and the OC value at $h(\mu) = -1$ is β. Because $\alpha = \beta$ and the normal distribution is symmetrical, the Monte Carlo results at $h(\mu) = \pm 1$ were pooled. The results were based on 40,000 iterations for each combination of $\alpha = \beta$ and δ_1 except for values at $\alpha = \beta = 0.05$ and 0.10 and $\delta_1 = 0.10$, which were based on 20,000 iterations.

Results showed that $\hat{\alpha}$ and $\hat{\beta}$ were always less than α and β and $\hat{ASN}$ values were always larger than ASN values. The errors in Wald's equations increased as δ_1 increased. The errors in Wald's ASN equation increased as $\alpha = \beta$ increased with no apparent trend for the errors in Wald's OC equation. The errors in Wald's equations are large for high values of δ_1.

An Example

Wald's OC and ASN equations were compared with Monte Carlo $\hat{OC}$ and $\hat{ASN}$ functions for several values of $h(\mu)$ for the lodgepole needleminer sequential sampling plan with $\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$ and $\beta = 0.10$ (table 4, figs. 3 and 4). In general, Wald's OC equation underestimated the actual OC function near μ_0 ($\mu < 10$) and overestimated it near μ_1 ($\mu \geq 10$) with $\hat{\alpha} = 0.036$ and $\hat{\beta} = 0.073$. Wald's ASN equation always underestimated the actual ASN function; the largest error was near $h(\mu) = 0$ where ASN reaches a maximum. The errors in Wald's equations were moderately serious for this example even though $\delta_1 = 0.64$ is not large.

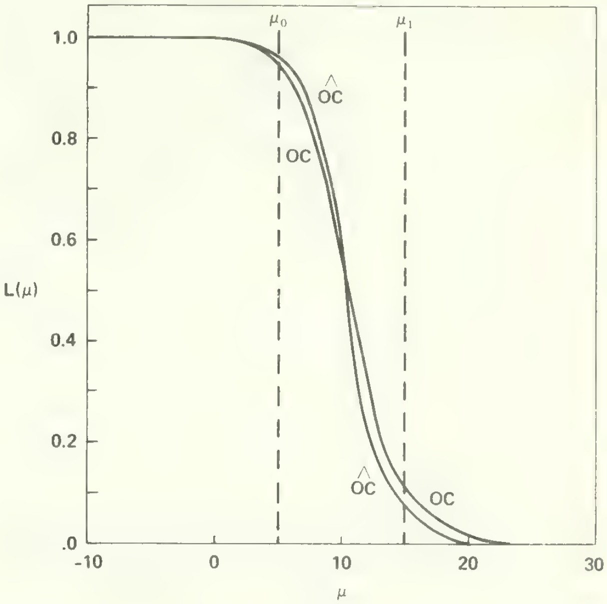

Figure 3. — *Comparison of Wald's and the Monte Carlo Operating Characteristic (OC) functions for the lodgepole needleminer sequential sampling plan (table 4).*

Table 4. — *Comparison of Wald's and Monte Carlo Operating Characteristic (OC) and Average Sample Number (ASN) values for several values of h(μ) and μ for the lodgepole needleminer sequential sampling plan ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$)*

$h(\mu)$	μ	OC				ASN						
		OC	$\hat{OC}$	$SD_{\hat{OC}}$	$OC-\hat{OC}$	ASN	$\hat{ASN}$	$SE_{\hat{ASN}}$	RE_{ASN}	R_{DSN}[1]	[1]$\hat{\gamma}_1$	[1]$\hat{\gamma}_2$
4	-10	1.000	1.000			2.75	3.40	0.04	-0.19	1-11	1.25	2.61
3	- 5	1.000	1.000			3.66	4.57	.07	- .20	1-17	1.64	4.11
2	0	0.997	1.000		-0.003	5.45	6.66	.13	- .18	1-33	1.70	4.02
1	5	.950	0.964	0.003	- .014	9.73	11.84	.12	- .18	1-74	1.84	4.98
0.5	7.5	.828	.866	.011	- .038	13.32	17.11	.44	- .22	1-80	1.88	4.89
.25	8.75	.711	.749	.014	- .038	14.96	19.11	.50	- .22	1-97	1.99	5.52
0	10	.562	.557	.016	+ .005	15.88	21.58	.56	- .26	1-95	1.74	3.88
- .25	11.25	.405	.392	.015	+ .013	15.76	19.73	.48	- .20	1-92	2.05	7.22
- .5	12.5	.268	.211	.013	+ .057	14.73	19.20	.48	- .23	1-100	2.12	6.26
-1	15	.100	.073	.004	+ .027	11.60	14.35	.14	- .19	1-94	1.78	4.63
-2	20	.011	.001	.001	+ .10	6.91	8.17	.14	- .15	1-35	1.61	3.78
-3	25	.001	.001	.001		4.69	5.45	.07	- .14	1-18	1.29	2.86
-4	30	.000	.000			3.53	4.23	.05	- .16	1-13	1.20	2.87

[1] R_{DSN}=range of the decisive sample number; $\hat{\gamma}_1$=skewness coefficient; $\hat{\gamma}_2$= kurtosis coefficient.

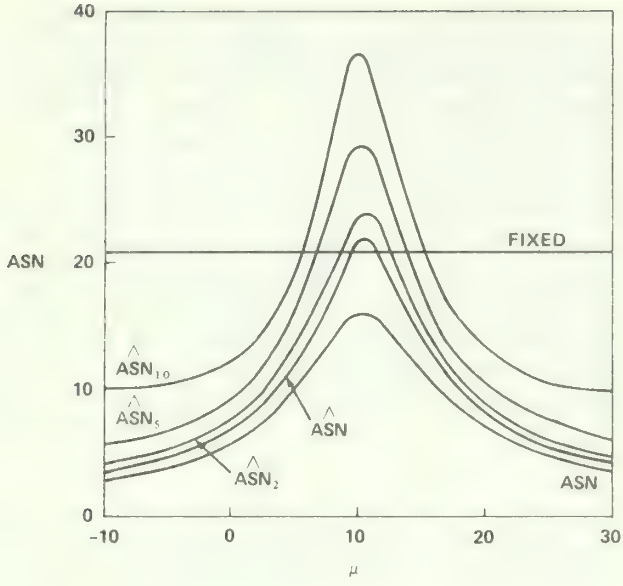

Figure 4. — *Comparison of Monte Carlo Average Sample Number ($\hat{ASN}$) functions for sequential sampling plans with $\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$, for numbers of observations taken at each stage of the plan equal to 1, 2, 5, and 10. The ASN function for the fixed sample size plan with equal reliability is also shown.*

It must be remembered that the ASN value is the average number of observations needed to make a terminating decision. The number of observations needed to make a terminating decision for one sample is a random variable called the decisive sample number (DSN), and the ASN is the mean of this random variable. The seriousness in the errors of Wald's equations can be better shown by looking at the distribution of the DSN (table 4, fig. 5). The distributions of DSN are skewed to the right; the skewness increases as $\hat{ASN}$ increases. The number of observations needed to make a decision for a particular sequential sample can be much larger than $\hat{ASN}$.

Procedure to Obtain More Accurate OC and ASN Functions

Monte Carlo results for the normal distribution showed that the errors inherent in Wald's OC and ASN equations can be large and are a function of the difference between the pest density levels or class limits ($\delta_1 = (\mu_1 - \mu_0)/\sigma$) and associated error probabilities used to construct a given sequential sampling plan. The practical consequences of these errors are (1) the actual error probabilities can be smaller than the nominal error probabilities used to build the sampling plan, and (2) more field observations are made than necessary. If sampling is destructive, time consuming, expensive, and/or early decisions are desirable, the consequences of these errors can be severe. Monte Carlo procedures should be used to determine if these errors are serious for a given sampling plan, and if they are, new sequential sampling plans should be developed to yield actual error probabilities, and resulting OC and ASN functions, approximately equal to the nominal ones desired.

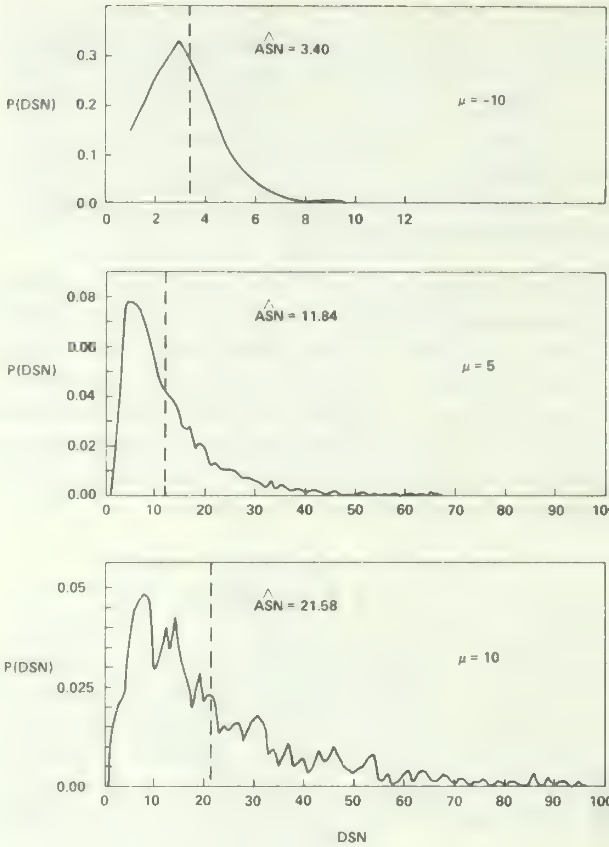

Figure 5. — *Empirical distributions of the Decisive Sample Number (DSN) for three values of μ for Wald's Sequential Probability Ratio Test (SPRT) with $\alpha = 0.05$ and $\beta = 0.10$. The dashed line shows the mean Average Sample Number ($\hat{ASN}$) for each DSN distribution.*

In developing a sequential sampling plan, Monte Carlo $\hat{OC}$ and $\hat{ASN}$ functions should be obtained for the decision boundaries based on the nominal values of α and β. If $\hat{\alpha}$ and $\hat{\beta}$ are close enough to α and β and Wald's and the Monte Carlo OC and ASN functions are similar, the Monte Carlo functions should be used to describe the operation of the sequential sampling plan. If the errors associated with Wald's equations are serious, new nominal values of $\alpha(\alpha')$ and $\beta(\beta')$ should be determined to yield new Monte Carlo estimates $\hat{\alpha}'$ and $\hat{\beta}'$ that are approximately equal to the desired (old nominal values) of α and β. Monte Carlo $\hat{OC}'$ and $\hat{ASN}'$ functions can then be obtained for the new sequential sampling plan based on the new nominal error probabilities α' and β'. If $\hat{\alpha}'$ and $\hat{\beta}'$ are not close enough to α and β, as many iterations of this procedure as are necessary to yield the desired Monte Carlo values of $\hat{\alpha}'$ and $\hat{\beta}'$ should be used. Usually one or two iterations will be sufficient.

Considering the lodgepole needleminer problem, if the difference between the Monte Carlo $\hat{OC}$ and $\hat{ASN}$ functions with $\hat{\alpha} = 0.036$ and $\hat{\beta} = 0.073$ and Wald's OC and ASN functions with $\alpha = 0.05$ and $\beta = 0.10$ (table 4, figs. 3 and 4) are not considered important, then the Monte Carlo $\hat{OC}$ and $\hat{ASN}$ functions should be used to describe the operation of the original sampling plan based on $\alpha = 0.05$ and $\beta = 0.10$.

If the errors in Wald's equations are considered serious, a new sampling plan should be constructed. $\hat{\alpha}$ and $\hat{\beta}$ were determined to be 0.035 and 0.072, respectively, based on 20,000 iterations each. To determine new nominal values α' and β' that yield new Monte Carlo values $\hat{\alpha}'$ and $\hat{\beta}'$ that are approximately equal to the desired old nominal values α and β, $\alpha' = (\alpha/\hat{\alpha})\alpha = \alpha^2/\hat{\alpha}$ and $\beta' = (\beta/\hat{\beta})\beta = \beta^2/\hat{\beta}$. For our example, $\alpha' = (0.05)^2 / 0.035 = 0.0714$ and $\beta' = (0.10)^2/0.072 = 0.1389$. Using these new nominal values, new decision boundaries can be developed for a new sequential sampling plan and Monte Carlo $\hat{OC}'$ and $\hat{ASN}'$ functions can be obtained (table 5). $\hat{\alpha}' = 0.051$ with $SD_{\hat{\alpha}'} = 0.003$, and $\hat{\beta}' = 0.097$ with $SD_{\hat{\beta}'} = 0.004$. Notice the difference between the $\hat{ASN}'$ values for the new sampling plan and the $\hat{ASN}$ values for the old sampling plan (table 4). Also, compare the empirical distribution of DSN′ of the new sampling plan (table 5, fig. 6) with the empirical distributions of DSN for the old sampling plan (table 4, fig. 5) for $\mu = -10$, 5, and 10.

Notice the close agreement between $\hat{OC}$ and $\hat{ASN}'$ of the new plan and OC and ASN of the old plan. A comparison of the $\hat{ASN}'$ function of the new sampling plan ($\hat{\alpha}' = 0.051$, $\hat{\beta}' = 0.097$) (table 5), which is closely approximated by the ASN function of the old sampling plan (fig. 4), with the ASN function of the fixed sample size Z - test sampling plan (FIXED, $\alpha = 0.05$, $\beta = 0.10$, $n = (Z_{\alpha} + Z_{\beta})^2/\delta_1^2 \simeq 21$) is more valid than the comparison with the $\hat{ASN}$ function of the old sampling plan ($\hat{\alpha} = 0.035$, $\hat{\beta} = 0.072$). This comparison is also more in favor of the sequential procedure.

Table 5. — *Monte Carlo Operating Characteristic (OC) and Average Sample Number (ASN) values for several values of h(μ) and μ for the lodgepole needleminer sequential sampling plan ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha' = 0.0714$, and $\beta' = 0.1389$)*

h(μ)	μ	OC		ASN					
		$\hat{OC}'$	$SD_{\hat{OC}'}$	$\hat{ASN}'$	$SE_{\hat{ASN}'}$	$SD_{DSN'}$	$R_{DSN'}$	$\hat{Y}_1'$	$\hat{Y}_2'$
4	-10	1.000		3.07	0.04	1.36	1-9	1.16	1.76
3	- 5	1.000		4.01	.06	2.25	1-15	1.48	3.48
2	0	0.993	0.002	5.70	.11	3.99	1-23	1.43	2.41
1	5	.949	.003	9.97	.10	8.66	1-63	1.77	4.24
0.5	7.5	.818	.012	14.07	.38	13.82	1-75	2.34	8.90
.25	8.75	.726	.014	14.51	.38	15.76	1-91	2.21	8.09
0	10	.568	.016	16.40	.42	17.57	1-91	1.88	5.38
- .25	11.25	.407	.016	16.61	.40	15.25	1-88	1.71	3.75
- .5	12.5	.255	.014	14.68	.35	15.28	1-79	1.65	3.32
-1	15	.097	.004	11.92	.12	9.83	1-67	1.75	4.30
-2	20	.012	.003	7.16	.12	4.38	1-25	1.38	2.45
-3	25	.001	.001	4.81	.07	2.35	1-18	1.40	3.26
-4	30	.000		3.70	.05	1.55	1-13	1.40	3.61

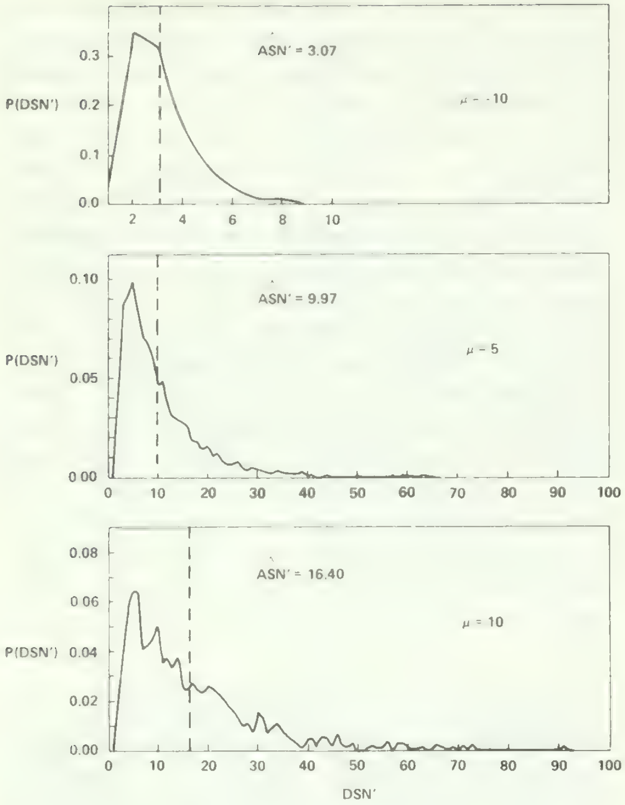

Figure 6. — *Empirical distributions of the Decisive Sample Number (DSN') for three values of μ for Wald's Sequential Probability Ratio Test (SPRT) with* $\alpha' = 0.0714$ *and* $\beta' = 0.1389$. *The dashed line shows the mean Average Sample Number (*$\widehat{\text{ASN}}$*) for each DSN distribution.*

MODIFICATIONS OF WALD'S SPRT

Many forest researchers (Cole 1960; Connola *et al.* 1959; Ives 1954; Ives and Prentice 1958; Knight 1960a, b; Tostowaryk and McLeod 1972) have modified the decision process of sequential sampling plans based on Wald's SPRT by taking more than one observation at each stage of the plan, not making a terminating decision until some minimum number of observations has been taken, and/or forcing a terminating decision to be made at some maximum number of observations. These deviations from the assumptions of Wald's SPRT will, of course, affect the actual OC and ASN functions of the modified sampling plan. However, in all forest applications where one or more of these modifications are made, Wald's OC and ASN equations are still used to describe the properties of the modified sampling plan.

To investigate the effects of these modifications on the accuracy of Wald's equations in describing the actual OC and ASN functions of the modified sampling plans, Monte Carlo $\widehat{\text{OC}}$ and $\widehat{\text{ASN}}$ functions were obtained for the following sampling plans for the lodgepole needleminer example ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, $\beta = 0.10$):

(1) Wald's SPRT with no modifications.
(2) Wald's SPRT with 2, 5, and 10 observations taken at each stage.
(3) Wald's SPRT truncated at 10, 16, and 21 observations.
(4) Wald's SPRT with terminating decisions first possible at a minimum of three and five observations (minimum points).
(5) Wald's SPRT with (a) a minimum point of 5, (b) a truncation point of 10, (c) a minimum point of 5 and a truncation point of 10, and (d) a minimum point of 5, a truncation point of 10, and 5 observations at each stage.

To obtain $\widehat{\text{OC}}$ and $\widehat{\text{ASN}}$ values, 5,000 and 1,000 iterations were used for each sampling plan at $h(\mu) = \pm 1$ and $h(\mu) \neq \pm 1$, respectively.

Two to 10 observations taken at each stage represent the range encounter in forestry sampling plans. A truncation point of 16 was obtained using Water's (1974) suggestion of using the maximum of Wald's ASN function as the maximum point, and a truncation point of 21 was obtained from Wald's (1947) rule for truncation, which is to use the sample size of the equally reliable ($\alpha = 0.05$, $\beta = 0.10$) fixed sample size Z - test as the maximum point. A truncation point of 10 is approximately the average truncation point encountered in forestry sampling plans — Wald's ASN value at $h(\mu) = 1$. If a terminating decision has not been made when the truncation point is reached, the average of the acceptance and rejection value at that stage is used as the decision point. The largest minimum point used in forestry sampling plans is 5.

Monte Carlo results were obtained with the ame starting seed value for the random number enerator for sampling plans with number of bservations equal to 1, 2, 5, and 10; truncation oints of 10, 16, and 21; and a minimum point of . Monte Carlo results were also obtained for ampling plans with number of observations qual to 1 and a minimum point of 5 using a dif-erent starting seed. This was done to reduce Monte Carlo variability in comparing the dif-erent modified sampling plans and to show Monte Carlo variability in the case of the OĈ nd AŜN values for Wald's SPRT (number of bservations = 1) (table 6).

The Monte Carlo results showed that $\hat{\alpha}$ and $\hat{\beta}$ ecome smaller and the associated AŜN values t h(μ) = ± 1 becomes larger as the number of bservations taken at each stage, truncation oint, or minimum point increase (table 6). hese trends are distinct for the range of umber of observations taken at each stage and he truncation points considered and slight for he range of minimum points considered. The Monte Carlo variability in estimating $\hat{\alpha}$ and $\hat{\beta}$ vas larger than the Monte Carlo variability in stimating the associated AŜN values at (μ) = ± 1 for Wald's SPRT with no modificaions.

The AŜN functions increased substantially as he number of observations at each stage in-reased, and the AŜN functions decreased subtantially as the truncation point decreased (figs. 4 and 7). Wald's SPRT with Wald's truncation point (21) yielded as AŜN function closer to the AŜN function of Wald's unmodified SPRT than both Wald's SPRT with Water's truncation point (16) or the average truncation point used in forestry examples (10). However, the AŜN function is still larger than the AŜN$_{21}$ function for $5 \leq \mu \leq 15$.

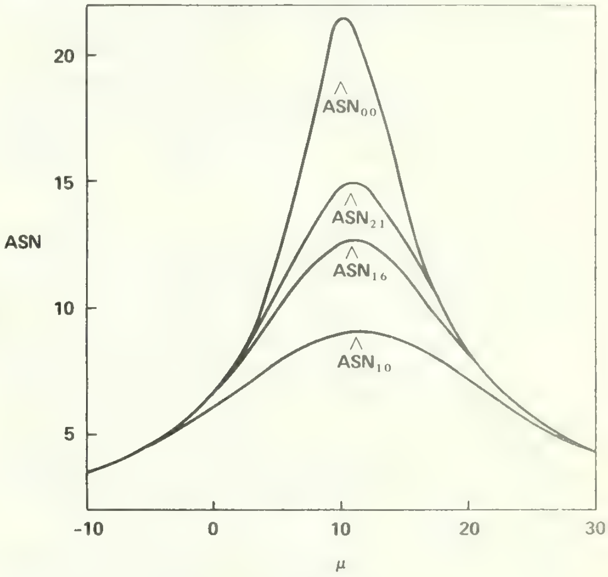

Figure 7. — *Comparison of Monte Carlo Average Sample Number (AŜN) functions for sequential sampling plans ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$) for truncation points of $N = 10$, 16, 21, and ∞.*

Table 6. — *Comparison of Monte Carlo values of α and β and Average Sample Numbers (ASN's) at h(μ) = ± 1 for sequential sampling plans ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$) for various numbers of observations taken at each stage of the plan, various truncation points, or various minimum number of observations*

h(μ)	L(μ)	Number of observations					Truncation points			Minimum number of observations	
		1	1[1]	2	5	10	10	16	21	3[1]	5
1	$\hat{\alpha}$[2]	0.036	0.032	0.031	0.023	0.020	0.123	0.077	0.061	0.032	0.035
	AŜN	11.84	11.86	13.19	15.54	18.84	7.86	9.87	10.74	11.89	12.22
-1	$\hat{\beta}$[3]	.073	.071	.066	.049	.031	.202	.140	.111	.071	.069
	AŜN	14.35	14.27	15.22	17.60	21.25	8.62	11.28	12.53	14.28	14.58

[1] Based on a different Monte Carlo run than the other Operating Characteristic (OĈ) and AŜN values.
[2] $\hat{\alpha} = 1 - \hat{OC} = 1 - L(\mu)$ for h(μ) = 1.
[3] $\hat{\beta} = \hat{OC} = L(\mu)$ for h(μ) = -1.

Monte Carlo results were obtained with the same starting seed value for Wald's unmodified SPRT and for Wald's SPRT with one observation at each stage and (a) a minimum point of 3, (b) a truncation point of 10, and (c) a minimum point of 3 and a truncation point of 10 (table 7). Monte Carlo results were also obtained with a different starting seed value for Wald's unmodified SPRT and for Wald's SPRT with one observation taken at each stage and (a) a minimum point of 5, (b) a truncation point of 10, and (c) a minimum point of 5 and a truncation point of 10. Monte Carlo results were also obtained for Wald's SPRT with 5 observations taken at each stage, a minimum point of 5, and a truncation point of 10.

The Monte Carlo results showed that in comparison to Wald's unmodified SPRT:

(1) a minimum point decreased $\hat{\alpha}$ and $\hat{\beta}$ and increased the associated A$\hat{S}$N values at $h(\mu) = \pm 1$ with these effects increasing slightly as the minimum point increased from 3 to 5;

(2) a truncation point increased $\hat{\alpha}$ to $\hat{\beta}$ and decreased the associated A$\hat{S}$N values at $h(\mu) = \pm 1$;

(3) the effects of a minimum and a truncation point above and beyond the effects of a truncation point are none to small decreases in $\hat{\alpha}$ and $\hat{\beta}$ and small increases in the associated A$\hat{S}$N values at $h(\mu) = \pm 1$ with these effects increasing slightly a the minimum point increased from 3 to 5;

(4) the effects of more than one observation a each stage above and beyond the effects o a truncation and minimum point are decreases in $\hat{\alpha}$ and β and increases in the associated A$\hat{S}$N values at $h(\mu) = \pm 1$.

The three modifications of Wald's SPRT considered in this paper definitely affect the accuracy of Wald's equations in describing the actua OC and ASN equations of the modified samplin plans. The size of the errors in Wald's equation depends on how far these modifications deviat from the assumptions of Wald's SPRT and wha combination of modifications are used.

CONCLUDING REMARKS

Assuming a normal distribution, a compariso of Wald's and Monte Carlo OC and ASN functions indicated that the errors inherent in Wald' equations can be serious. The practical consequences of these errors are: (1) the actual erro probabilities can be smaller than the nomina error probabilities used to build the samplin plan, and (2) more observations are usuall taken in the field than necessary. These error

Table 7. — *Comparison of Monte Carlo values of α and β and Average Sample Numbers (ASN's) at $h(\mu) = \pm 1$ for sequential sampling plans ($\mu_0 = 5$, $\mu_1 = 15$, $\sigma = 15.62$, $\alpha = 0.05$, and $\beta = 0.10$) for two Monte Carlo runs with various combinations of numbers of observations taken at each stage of the plan, truncation points, and minimum number of observations*

Run number		1					2			
No. of observations		1					1			5
Minimum[1]		1	3	1	3	1	5	1	5	
Truncation point[1]		∞		10		∞	∞	10		
$h(\mu) = 1$	$\hat{\alpha}$[2]	.032	.032	.115	.115	.036	.035	.123	.123	.119
	A$\hat{S}$N	11.86	11.89	7.84	7.88	11.84	12.22	7.86	8.19	9.01
$h(\mu) = -1$	$\hat{\beta}$[3]	.071	.071	.194	.194	.073	.069	.202	.200	.196
	A$\hat{S}$N	14.27	14.28	8.64	8.65	14.35	14.58	8.62	8.78	9.45

[1] A minimum of 1 indicates no minimum point, a truncation point of ∞ indicates no truncation point, and a minimum of 1 and a truncation point of ∞ indicates an unmodified sequential sampling plan.

[2] $\hat{\alpha} = 1 - \hat{OC} = 1 - L(\mu)$ for $h(\mu) = 1$.

[3] $\hat{\beta} = \hat{OC} = L(\mu)$ for $h(\mu) = -1$.

increase as the difference between the class limits $(\delta_1 = (\mu_1 - \mu_0)/\sigma)$ and associated error probabilities (α and β) used to build a sequential sampling plan increase. Similar results have been obtained for the binomial, negative binomial, and Poisson distributions.

Also assuming a normal distribution, Monte Carlo results indicate that any of the above modifications will affect the actual OC and ASN functions of the sequential sampling plan and thus decrease the accuracy of Wald's equations in describing these actual functions. The practical consequences of these modifications are (1) the actual error probabilities decrease and the ASN function increases as the number of observations taken at each stage increases, (2) the actual error probabilities increase and the ASN function decreases as the truncation point decreases, and (3) the actual error probabilities decrease and the ASN function increases as the minimum point increases. Similar results would be obtained for the binomial, negative binomial, and Poisson distributions.

Regardless of what distribution and whether no or any combination of the above modifications were used in developing a sampling plan based on Wald's SPRT, I strongly suggest that Monte Carlo $\hat{O}C$ and $A\hat{S}N$ functions be obtained for the decision boundaries of the original SPRT. If $\hat{\alpha}$, $\hat{\beta}$, and the Monte Carlo functions are considered to be not seriously divergent from α, β, and Wald's equations, then the Monte Carlo functions should be used to describe the actual functions of the original sampling plan.

If, on the other hand, the differences between Wald's and Monte Carlo results are substantial, a new sampling plan should be developed using the procedure presented in this paper so that the Monte Carlo values $\hat{\alpha}'$ and $\hat{\beta}'$ of the new plan are approximately equal to the nominal values α and β of the old plan. Monte Carlo $\hat{O}C'$ and $A\hat{S}N'$ functions should then be obtained for the decision boundaries of the new plan and used to describe the actual functions.

Given the budget available, the time and cost of taking observations, whether sampling is destructive or not, and the importance of early decisions, the forest researcher will have to decide whether to use fixed sample size or sequential sampling plans. If a sequential sampling plan is used, the forest researcher then must decide whether to construct the new or old sequential sampling plan and associated Monte Carlo $\hat{O}C$ and $A\hat{S}N$ functions. The only fair comparison is between the fixed sample size and the new sequential sampling plan. For either sequential sampling plan, the cost of obtaining $\hat{O}C$ and $A\hat{S}N$ functions is inexpensive.

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A COMPARISON OF TWO METHODS USED TO ESTIMATE STAND STOCKING IN UPLAND CENTRAL HARDWOODS

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The term stand stocking used in this paper refers to the density of trees in a stand expressed by the formula given by Gingrich (1967)[1]:

Stand Stocking Percent (SSP) =

$$(-0.0507N + 0.1698\,\Sigma D + 0.0317\,\Sigma D^2)/10$$

where

N = number of trees per acre

ΣD = sum of their individual diameters

ΣD^2 = sum of the squares of their diameters.

Each tree in the stand must be tallied and measured to derive stocking percent using the above equation. This process is time consuming, so sampling methods are used to estimate the quantities needed for the stocking equation.

One sampling method, which I call "variable plus fixed area sampling" (F), provides an estimate of basal area from the variable area plot and an estimate of the number of trees from the fixed area plot with origin in common with the point.

Typically, the fixed area plot is circular with 1/20 acre area. Thus

BA = basal area/acre = BAF x k = basal area factor x point sample tree count

n = no. of trees/acre = fixed plot tree count/fixed area plot size

D_{bf} = diameter of tree of average basal area

$$= ((\mathrm{BAF} \times k)/0.005454\,n)^{1/2}$$

Now substituting

$$N = n$$

$$\Sigma D = nD_{bf}$$

$$\Sigma D^2 = (\mathrm{BAF} \times k)/0.005454$$

into Gingrich's equation we have

$$SSP = (-0.0507n + 0.1698nD_{bf} + (0.0317\mathrm{BAF}\ k)/0.005454)/10$$

or

$$SSP = -0.00507n + 0.2299\,n\left((\mathrm{BAF} \times k)/n\right)^{1/2} + 0.58122\,\mathrm{BAF} \times k.$$

The second method uses only the trees sampled from a variable area plot. In this case sample tree diameters must be measured.

Thus

$$n = \sum_{i=1}^{k} \mathrm{BAF}/0.005454d_i^2 \quad i = 1, 2, \ldots, k;\ k \text{ sample trees}$$

$$= (\mathrm{BAF}/0.005454)\sum_{i=1}^{k} 1/d_i^2$$

$$\Sigma D = \sum_{i=1}^{k} (\mathrm{BAF}/0.005454d_i^2)\,d_i$$

$$= (\mathrm{BAF}/0.005454)\sum_{i=1}^{k} 1/d_i$$

$$\Sigma D^2 = \Sigma(\mathrm{BAF}/0.005454d_i^2)\,d_i^2$$

$$= (\mathrm{BAF} \times k)/0.005454$$

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[1] *Gingrich, S. F. 1967. Measuring and evaluating stocking and stand density in upland hardwood forests in the Central States. For. Sci. 13:38-53.*

and substituting

$$SSP = \left(-0.0507 \frac{BAF}{0.005454} \sum_{i=1}^{k} \frac{1}{d_i^2} + 0.1698 \frac{BAF}{0.005454} \sum_{i=1}^{k} \frac{1}{d_i} + 0.0317 \frac{BAF * k}{0.005454} \right) / 10$$

or

$$SSP = \frac{BAF}{10} \left(5.8122k + 31.1331 \sum_{i=1}^{k} \frac{1}{d_i} - 9.2959 \sum_{i=1}^{k} \frac{1}{d_i^2} \right)$$

Note that when BAF = 10 then

$$SSP = 5.8122k + 31.1331 \sum_{i=1}^{k} \frac{1}{d_i} - 9.2959 \sum_{i=1}^{k} \frac{1}{d_i^2}.$$

Frequently, in addition to stocking we need to know the diameter of the tree of average basal area. For the variable plus fixed plot method this is

$$D_{bf} = \left(\frac{k * BAF}{0.005454n} \right)^{1/2}$$

and for the variable plot method is

$$D_{bv} = \left(\frac{k}{\frac{1}{d^2}} \right)^{1/2}$$

The stocking and average diameter equations differ in each method by the way in which the number of trees per acre are obtained. These differences affect the estimate obtained by each method. From these equations we can see that the variability of point sample estimates increase as the variability of tree diameters increase among points whereas among plots the variability of estimates are related to the variability in the number of trees sampled among plots.

Thus the variability of stocking and average diameter estimates is sensitive to the distribution of tree diameters within a stand. To see how each method compares in its ability to estimate stocking and average diameter in stands with different diameter distributions, I simulated the sampling process on a computer using four stands that had different diameter distributions (fig. 1). Trees were located randomly within each stand. Then for each stand 10 points were selected and 1/20 acre circular plots were located with their center at each point. For each sampling method stand stocking percent and mean stand diameter were averaged over the 10 points. This procedure was repeated 100 times while keeping tree location constant. In addition, stocking and average diameter were calculated using all trees in the stand and these were designated as true values.

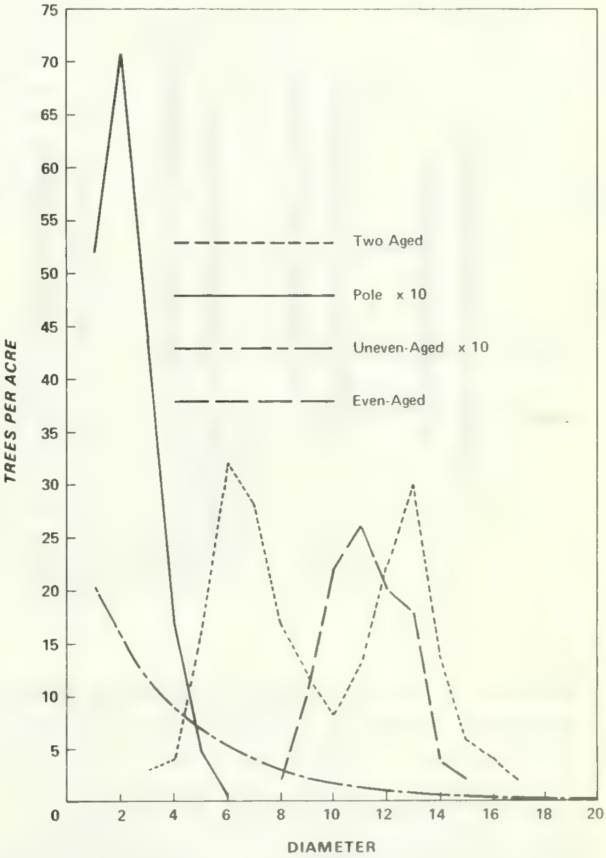

Figure 1. — *Diameter structures of two aged, pole, uneven-aged, and even-aged stands.*

Each method estimated stocking percent with about the same accuracy except the uneven-aged stand was estimated more closely by the variable plus fixed plot method (fig. 2). The variable plot method deviated farthest (under-estimated) true stocking percent and had a variance 1⅓ times greater than that of the variable plus fixed plot method for the uneven-aged stand.

The comparison of average diameter revealed that the methods were similar in their estimates for the two-aged and pole-sized stands (fig. 3). But, their estimates were not similar for the even- and uneven-aged stands. In uneven-aged stands estimates obtained from the point sample are biased upward and the variance is 3½ times larger than for the point plus fixed plot method. In the even-aged stand the pattern in variance is reversed, but estimates are not biased.

Therefore, point sampling methods alone should not be used to estimate stocking and average diameter in uneven-aged stands. But the point sampling method can be used to provide estimates of stocking and average stand diameter in stands having distributions similar to the other three studied with a reliability equal to or better than the combination method. In particular, for stands having diameter distributions like the even-aged stand presented here, estimates of mean stand diameter obtained by point sampling tend to be more reliable than those obtained by using the combination method.

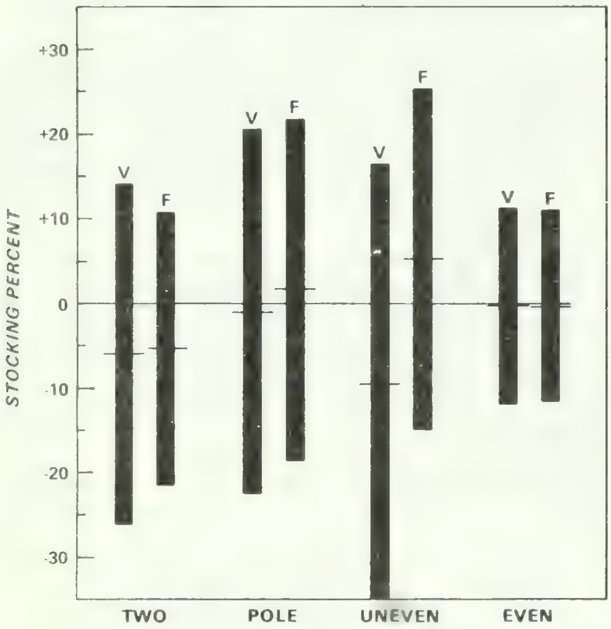

Figure 2. — *A comparison of stocking precent estimates based on 100 averages of 10 points in four stands using variable area plot (V) and variable area plot plus fixed area plot (F) sampling methods. Lines through bars represent estimates of true value of stocking percent (line at 0) and vertical scale shows deviation values.*

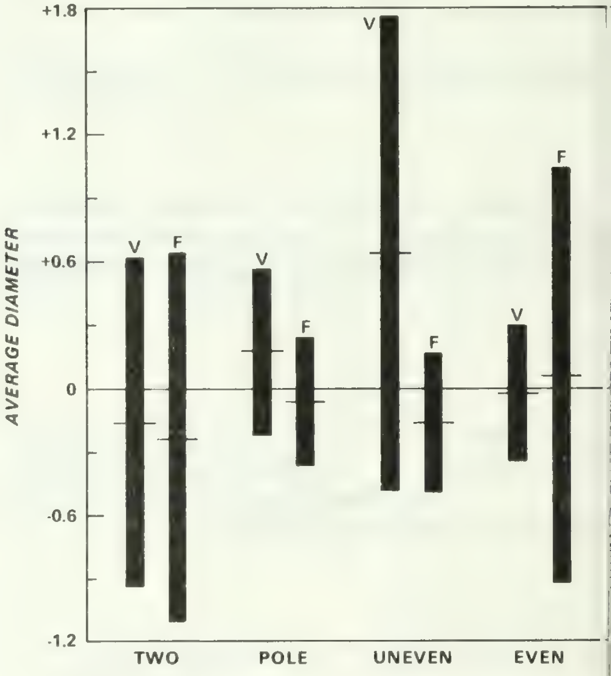

Figure 3. — *A comparison of mean stand diameter (tree of average basal area) estimates based on 100 averages of 10 points in four stands using variable area plot (V) and variable area plot plus fixed area plot (F) sampling methods. Lines through bars represent estimates of true value of mean stand diameter (line at 0) and vertical scale shows deviation values.*

NONLINEAR BASAL AREA GROWTH MODELS FOR RED PINE

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Previous models of individual tree growth have been based on the open-grown tree concept (Newnham 1964, Arney 1974, Ek and Monserud 1974) and on empirical functions (Bella 1971, Tennent 1975, Moore *et al.* 1973, Adlard 1974). In the open-grown tree approach, individual tree size is assumed to be maximum if the tree is grown in the open (free from competition); the maximum size is reduced if the tree is grown in a stand (subject to competition).

Most periodic growth models for individual trees express the amount of competition a tree receives from its neighbors. Many view competition between trees in terms of zones of influence (Staebler 1951, Newnham 1964, 1966, Opie 1968, Bella 1971, Gerrard 1969, Arney 1974, Keister 1971, Ek and Monserud 1974). The basic assumption is that competition between individual trees occurs only when their zones overlap.

The objectives of this study were to formulate nonlinear biological basal area growth models and to analyze the relation between individual tree competition and growth. We used data from an even-aged red pine plantation near Star Lake, Wisconsin.[1] Initial spacing of the plantation was 6 by 6 feet. Site index was 65 at age 50 and tree survival was high on the site (Wilson 1963).

FORMULATION OF NONLINEAR BASAL AREA GROWTH MODEL

Periodic basal area growth can be related to potential basal area increment when the immature tree is free from competition. This growth can then be reduced by a competition factor when the tree is grown under competition. This relation can be shown by the following equations:

$\Delta B = \Delta B^* [1 - e^{-k(1/c)m}]^N$ (1)
or $\Delta B = \Delta B^* e^{-kC}$ (2)
where ΔB = the periodic tree basal area growth of the tree,
ΔB^* = the potential growth when the tree is free from competition,
C = the competition index of the tree,
k, m, and N = growth factors such as site, species, age, and density.
As $C \uparrow$, $\Delta B \downarrow$; as $C \downarrow$; $\Delta B \uparrow$
$\lim_{C \to 0} \Delta B = \Delta B^*$ for $k > 0, m > 0$

$\lim_{C \to \infty} B = 0$ for intolerant species.

The advantage of the models (equations 1 and 2) is that they offer a logical explanation of the relation between the dependent and independent variables. However, the potential growth of a tree might not be realized not only because of competition, but also because of disease, insects, animals, wind, frost, etc. Furthermore, the model is less useful for predicting growth of intermediate and suppressed trees when they are completely released because these trees may not regain their full potential growth. So the condition that

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[1] *The data were provided by Dr. Alan R. Ek, University of Minnesota, College of Forestry, and Wisconsin Department of Natural Resources.*

$\Delta B \rightarrow \Delta B^*$ as $C \rightarrow 0$

may not be fully realized.

An alternative approach is to assume that tree periodic basal area growth is directly related to site, initial basal area, and functional crown surface, and inversely related to competition index. Functional crown surface is correlated with tree growth. Tree height or basal area are correlated with the functional crown surface for immature individual trees growing in dense even-aged stands (not stagnant) of single intolerant species. Therefore, in the case of lacking information on tree height and functional crown surface, initial tree basal area or diameter breast height and competition index may predict tree periodic basal area increment. For this study, we define two models similar to equations 1 and 2, except ΔB^* was replaced by "a B^b"; where B is the basal area of the tree at the beginning of the growth period and a and b are two additional factors.

MEASURE OF TREE COMPETITION

The competition imposed on a tree is measured by the distance to the competing tree, amount of overlap area, and relative size. It is formulated in the following manner:

$$C_i = (1/A_i) \sum_{j=1}^{N} 0_{ij} \, W_{ij} \qquad (3)$$

where C_i = the competition index of tree i,

A_i = the area of the influence zone or circle about the sample tree i with the radius (P_i) proportional to the tree diameter,

P_i = 1, 1.5, 2.0, 2.5,

O_{ij} = the area of overlap between tree i and its competitor j for j = 1, 2, . . ., N_i,

N_i = number of competitors of tree i,

W_{ij} = a weighting factor for O_{ij}.

We used the following weighting factor:

$$W_{ij} = R\,[\,1 - \exp(-k_1 r_{ij})]^n \qquad (4)$$

where

$r_{ij} = (d_j/d_i)^E$ and d_j/d_i is the ratio of diameters of tree i and its competitor j,

$R = \max\,(d_j/d_i)^E$ for all trees (i, j) with overlapping influence zones,

k_1 and E are factors related to species, age, site, and density (E = 1 to 4).

$$k_1 = -\log\,[\,1-(1/R)^{\frac{1}{n}}] \qquad (5)$$

when weighting factor $W_{ij} = 1$ is assigned for th condition $d_i = d_j$, n was assigned the value 1 or 2

As $r_{ij} \rightarrow 0$, $W_{ij} \rightarrow 0$;
$r_{ij} \rightarrow \infty$, $W_{ij} \rightarrow R$;

and as
$r_{ij} \rightarrow 1$, $W_{ij} \rightarrow 1$.

The weighting factor for modifying the overla area between a tree and its competitor should re flect the potential size difference of the sampl tree i and its competitor j.

RESULTS AND DISCUSSION

Approximately optimal values of Pi and E (fo equations 3 and 4) for standard error and corre ation of regression between basal area growt and competition index were derived via iteratio (table 1). Bella's (1971) index generated com parable results. When no iterations on E and were performed, i.e., E = n = 1 Chen's (1976 model resulted in correlations that were approx mately 10 percent higher. A modification o Gerrard's (1969) index (inclusion of the exponen E) proved somewhat inferior to the two othe indexes, but is easier to calculate. The indexe will have to be compared using different specie ages, and stand conditions.

For predicting individual tree growth one o the two proposed basal area growth models wa fitted via nonlinear regression (table 2). Th

Table 1. — *Correlation between periodic basal area growth and competition index for three competition models*[1]

Plot[2]	Observations		Coefficient of Determination[5]		Standard	Standard Regression Coefficients		
	Total[3]	Regression[4]	Adjusted	Unadjusted	error	a	b	k
					Inch^2			
1	186	17	0.55	0.85	2.84	34.63	-0.4571	1.5557
2	203	20	.52	.86	2.16	3.25	.1137	0.7839
3	269	19	.88	.95	0.52	0.043	1.2744	.2038
1, 2, & 3 combined	658	56	.60	.86	1.81	1.38	.3682	.7912
4	296	24	.56	.80	5.17	3134.23	-1.4585	1.9977

[1] $\Delta B = aB^b \left(\exp(-kC)\right)$

ΔB = the periodic tree basal area growth in square inches.

C = the competition index (equation 3) with weighting factor (equation 4).

Parameter E = 2, R = 1, n = 2 used for all in calculation of competition index.

[2] Stand age 32-37.

[3] Total observations used for calculating competition index.

[4] Number of trees for which growth and competition was determined.

[5] The coefficient of determination adjusted for the mean measures the contribution of the sample mean in explaining variance of the dependent variable.

Table 2. — *Nonlinear regression gits for a nonlinear basal area growth models*[1]

Plot[2]	r	Standard error	E[3]	Pi[4]	n	Remarks
Inch^2		*Inch*^{2}				
1	-0.82	1.26	2	1	2	Chen (1976) model
2	-0.72	1.41	2	2.5	1	$W_{ij} = (1-e^{-k_1 (d_j/d_i)^E})^n$
3	-0.73	1.60	2	1.0	2	(equation 4)
4	-0.70	2.42	1.5	1.0	2	
1	-0.82	1.27	3.5	1.0	-	Bella (1971)
2	-0.72	1.42	2.0	2.5	-	
3	-0.73	1.60	4.0	1.0	-	$W_{ij} = (d_j/d_i)^E$
4	-0.70	2.43	1.5	1.0	-	
1	-0.72	1.50	4	2.5	-	modified Gerrard index
2	-0.63	1.57	4	2.0	-	
3	-0.72	1.62	4	1.0	-	$C_i = \Sigma \left(\frac{O_{ij}}{A_i}\right)^E$ and
4	-0.63	2.63	2	1.0	-	$W_{ij} = 1$

[1] $\Delta B_i = ae^{-kC_i}$ or $\log \Delta B_i = \log a - kC_i$ where $C_i = \sum_{j=1}^{N_i} \frac{O_{ij}}{A_i} W_{ij}$ (competition index) and W_{ij} is a weighting factor.

[2] Plot age 32-37;plots 1 to 3 are control plots and plot 4 is a thinned plot.

[3] E = parameter of competition index

[4] Pi = proportionality factor for radius of zone of influence of subject tree and tree diameter.

model adequately explained basal area growth as a function of basal area and competition for the first three plots. The large standard error for the thinned plot (plot 4) indicates a much poorer fit.

Further work is underway to test those models using more plots and different species and ages. Preliminary results indicate less satisfactory fits for an older plot of the Star Lake plantation (age 58-65). Relative diameters or basal areas are adequate weighting factors only in some instances. It will be necessary to find weighting factors that better reflect the potential size increment of the sample tree i and its competitor j such as height, crown ratio, live crown length, or functional crown surface or volume. These variables may improve the growth models for red pine as well as for other species in even-aged stands. Species tolerance will have to be considered if the competition model is applied to mixed stands (Chen 1976).

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DISCRETE TIME MARKOV PROCESSES

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By observing the evolution of natural phenomena, it is readily apparent that events occur that are not entirely predictable. The modeling of such events is often facilitated by employing random processes. The intent of this paper is to consider and to illustrate a subclass of the set of stochastic processes — one known as discrete time Markov models. This subclass is termed discrete time because time is indexed in finite steps rather than as a continuum. Diameter class distributions in forest stands will be used to illustrate the process.

A Markov chain is a discrete time stochastic process consisting of a sequence of random events $\{X_1, X_2, X_3, \ldots\}$, each with a finite number of possible outcomes $\{a_1, a_2, \ldots, a_r\}$ (Phillips *et al.* 1976) This set of possible outcomes is termed state space. The value assumed by X_i is called the state of the process at time i. It is assumed that the random variable, X_i, depends only upon the previous event X_{i-1}, and affects only the subsequent one, X_{i+1}. This assumption, known as the Markov assumption, avoids having to express joint distributions for all events at one time. Instead, it is sufficient to express conditional distributions of just two neighboring random variables at a time. Markov's assumption simplifies the problem but does not completely eliminate the dependence between random variables. Therefore life processes can be realistically represented.

Given that $X_0 = a_i$ is the present state of a process, one desires to know the probability distribution of the possible outcomes for X_1. These transitional probabilities are designated p_{ij}, which represent the conditional probability of going from state a_i to state a_j after one step or transition, i.e., $P\{X_1 = a_j | X_0 = a_i\}$.

A conventional means of exhibiting transition probabilities is with a square matrix. A transition matrix for a three-state process may be represented as:

$$P = (p_{ij}) = \begin{array}{c} \\ a_1 \\ a_2 \\ a_3 \end{array} \begin{array}{c} \begin{array}{ccc} a_1 & a_2 & a_3 \end{array} \\ \left[\begin{array}{ccc} p_{1,1} & p_{1,2} & p_{1,3} \\ p_{2,1} & p_{2,2} & p_{2,3} \\ p_{3,1} & p_{3,2} & p_{3,3} \end{array}\right] \end{array}$$

Because each row of the above matrix represents a probability distribution for X_1, $\sum_j p_{ij} = 1$ for each i.

The matrix P completely describes the process for any given outcome at X_1 given its initial dependence upon X_0. If event X_1 is described, the probability distribution for X_2 must be developed. By the Markov assumption, the next state, X_2 in this instance, depends only upon the previous state, X_1. However, X_1 depends upon X_0. Three mutually exclusive paths exist to progress from $X_0 = a_1$ to $X_2 = a_1$ (fig. 1). The probability of being in state a_1 at time 2 given that the process was in state a_1 at time o may be represented as the sum of the three "path probabilities":

$$\begin{aligned} P\{X_0 = a_1 \rightarrow X_2 = a_1\} = & \\ & P\{X_0 = a_1 \rightarrow X_1 = a_1 \rightarrow X_2 = a_1\} \\ & + P\{X_0 = a_1 \rightarrow X_1 = a_2 \rightarrow X_2 = a_1\} \\ & + P\{X_0 = a_1 \rightarrow X_1 = a_3 \rightarrow X_3 = a_1\} \quad (1) \end{aligned}$$

By employing the Markov assumption and the matrix of one-step transition probabilities, Equation (1) can be rewritten as:

$$\begin{aligned} P\{X_0 = a_1 \rightarrow X_2 = a_1\} = & \\ & p_{1,1}\, P\{X_1 = a_1 \rightarrow X_2 = a_1\} \\ & + p_{1,2}\, P\{X_1 = a_2 \rightarrow X_2 = a_1\} \\ & + p_{1,3}\, P\{X_1 = a_3 \rightarrow X_2 = a_1\}. \end{aligned}$$

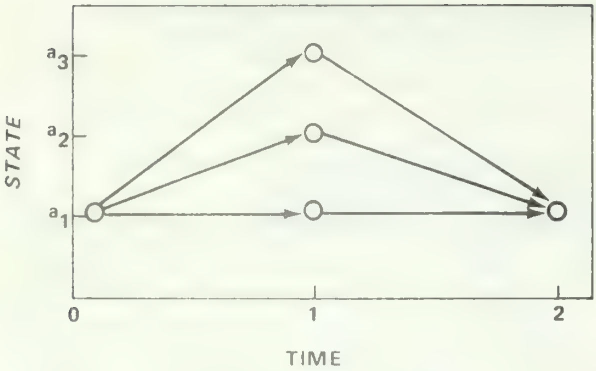

Figure 1. — Possible transitions from $X_0 = a_1$ *to* $X_2 = a_1$ *for a three-state process.*

The probability for the first leg of each path is readily obtained from the matrix of one-step probabilities. The probabilities for the second step of each path is really the transition probability associated with the second transition. At this point an additional simplifying assumption is needed. If it is assumed that the transitional probabilities do not change with time, then:

$$P\{ X_0 = a_1 \rightarrow X_2 = a_1 \} = p_{1,1}\,p_{1,1} + p_{1,2}\,p_{2,1} + p_{1,3}\,p_{3,1} . \quad (2)$$

The assumption is known as stationarity; without it the process would not be able to continue because a new transition matrix would be needed for each transition. Using similar logic, probabilities may be developed for other states at X_2 given that $X_0 = a_1$:

$$P\{ X_0 = a_1 \rightarrow X_2 = a_2 \} = p_{1,1}\,p_{1,2} + p_{1,2}\,p_{2,2} + p_{1,3}\,p_{3,2} . \quad (3)$$

$$P\{ X_0 = a_1 \rightarrow X_2 = a_3 \} = p_{1,1}\,p_{1,3} + p_{1,2}\,p_{2,3} + p_{1,3}\,p_{3,3} . \quad (4)$$

Thus, Equations (2), (3), and (4) specify the probability distribution of X_2, given that $X_0 = a_1$. Similarly, other expressions may be developed to specify the probability distribution for X_2 given that $X_0 = a_2$ or $X_0 = a_3$. The notation $p_{ij}^{(2)}$ is utilized for the individual elements of the two-step transition matrix and the complete two-step matrix, $P^{(2)}$, for the three-state process may be represented as:

$$P(2) = p_{ij}^{(2)})) \quad \begin{bmatrix} p_{1,1}^{(2)} & p_{1,2}^{(2)} & p_{1,3}^{(2)} \\ p_{2,1}^{(2)} & p_{2,2}^{(2)} & p_{2,3}^{(2)} \\ p_{3,1}^{(2)} & p_{3,2}^{(2)} & p_{3,3}^{(2)} \end{bmatrix}$$

As indicated above, the individual elements are calculated from the one-step matrix:

$$p_{1,1}^{(2)} = p_{1,1}\,p_{1,1} + p_{1,2}\,p_{2,1} + p_{1,3}\,p_{3,1} .$$

The two-step transition matrix is obtained by squaring the one-step matrix:

$$P^{(2)} = P \,.\, P = P^2 \quad (5)$$

The relation expressed in Equation (5) is only possible by use of the Markov and stationarity assumptions.

To obtain the distributions of X_3 given various possible states of X_0, it is again necessary to consider possible paths that lead from X_0 to X_3 in a similar fashion as was illustrated for X_2. Following that logic, the elements of the three-step transition matrix can be written in terms of the two-step and one-step probabilities:

$$p_{1,1}^{(3)} = p_{1,1}^{(2)}\,p_{1,1} + p_{1,2}^{(2)}\,p_{2,1} + p_{1,3}^{(2)}\,p_{3,1} .$$

In matrix notation that is:

$$P^{(3)} = p^{(2)} \,.\, p = p^2 \,.\, p = p^3 .$$

The n-step transition matrix is equal to the one-step transition matrix raised to the n^th^ power,

$$P^{(n)} = P^{n} . \quad (6)$$

The relation expressed by Equation (6) is the most important result for Markov chains because it gives the probability of being in a particular state at a particular time, given the initial state.

To illustrate the use of the discrete time Markov model, data were obtained from permanent growth plots in a central Wisconsin mixed hardwood stand that had been measured for diameter for 19 consecutive years. The 25 states chosen for the model are the 1-inch diameter classes from 8-inch through 29-inch, a diameter class called > 29 inch, and the categories of death and harvest. The 8-inch class was the lowest diameter class in which all trees were measured and

31-inch was the largest diameter of any tree after 19 years. Because only the first nine growth periods were utilized to develop the model, it was necessary to define the largest diameter class as > 29 to obtain numerical values for the transition probabilities.

A tree in any state representing a diameter class may either remain in that class, move to a higher class, die, or be harvested. The dead and harvest states are considered absorbing states because once a tree has entered either one of these states it cannot leave it. The 1-inch diameter classes are termed transient states.

The information to determine the probabilities for transitions between states and to verify the predictive ability of the model was obtained by summarizing the progression of the initial trees in each diameter class for the 19-year period (table 1). Ingrowth trees were not included in the summaries.

If a tree was in the 10-inch diameter class 9 years ago, the transition probabilities associated with its movement are determined as follows: (1) the tree will remain in the 10-inch class, $p_{1,0,1,0}$, = 44/139; (2) the tree will advance to the 11-inch class, $p_{1,0,1,1}$, = 81/139; (3) the tree will move into the 12-inch class, $p_{1,0,1,2}$, = 5/139; (4) the tree will die, $p_{1,0,m}$ = 8/139; or (5) the tree will be harvested, $p_{1,0,c}$ = 1/139.

The transition probabilities for the other diameter classes are similarly determined with the respective diameter class progression summaries. Because death and harvest are absorbing states, $p_{m,m} = p_{c,c} = 1$ (table 2).

As indicated by Equation (5), the two-step transition probabilities are obtained by squaring the initial transition matrix. The numbers $p_{ij}^{(2)}$ for i and j = 8 . . . 29, > 29, M[1], and C given the probability of a tree being in state j given that it was in state i two steps ago (table 3).

If $t^{(0)} = (t_8^{(0)}, t_9^{(0)}, \ldots, t_{29}^{(0)}, t_{>29}^{(0)}, t_m^{(0)}, t_c^{(0)})$ is a vector whose elements correspond to the initial number of trees in each state, then the matrix of two-step transition probabilities can be used to predict the disposition of those initial trees after 18 growing seasons. The numbers $p_{im}^{(2)}$ and $p_{i,c}^{(2)}$ for i = 8 . . . 29, > 29 are, respectively, the death and harvest probabilities for a tree given that it was initially in the i^{th} diameter class. The predicted number of mortality trees, m_i, and harvested trees, c_i, are:

$$m_i = t_i^{(0)} \cdot p_{i,m}^{(2)} \qquad (7)$$

and

$$c_i = t_i^{(0)} \cdot p_{ic}^{(2)} \text{ for } i = 8 \ldots 29, > 29. \qquad (8)$$

Because Equations (7) and (8) account for death and harvest, the number of surviving trees, s_i, from each initial diameter class is

$$s_i = t_i^{(0)} \cdot (1 - p_{i,m}^{(2)} - p_{ic}^{(2)}) \qquad (9)$$
$$\text{for } i = 8 \ldots 29, > 29.$$

Equation (9) indicates the number of trees in the i^{th} diameter class expected to survive. It does not indicate the distribution of the surviving trees.

To determine the diameter distribution for surviving trees it is necessary to sum all the ways that a tree can enter a diameter class, regardless of its initial class:

$$t_j^{(2)} = \Sigma_i t_i^{(0)} \cdot p_{ij}^{(2)} \qquad (10)$$

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[1] *M = dead trees; C = harvested trees.*

Table 1. — *The progression of all trees initially in the 10-inch diameter class by number of trees and change in diameter class*
(In number of trees)

Diameter class (in.)	Measurement																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
10	139	133	115	107	98	83	69	62	61	44	41	35	29	25	22	19	16	15	13
11	0	5	23	31	37	50	61	68	68	81	75	75	69	67	66	67	67	60	56
12	0	0	0	0	0	0	2	2	2	5	12	18	29	34	35	36	37	38	38
13	0	0	0	0	0	0	0	0	0	0	2	2	2	2	3	4	6	10	12
14	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	2	2	2
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total	139	138	138	138	135	133	132	132	131	130	130	130	129	129	128	128	128	125	122
Total mortality		1	1	1	4	6	7	7	7	8	8	8	9	9	10	10	10	13	15
Total cut		0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	2

Table 2. — *The initial matrix of transition probabilities based on ratios from measurements 1 and 10*

Diameter class: at measurement 1 (inches)	Diameter class at measurement 10 (inches)																							M[1]	C[1]
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	>29		
8	0.37	0.48	0.04																					0.09	0.01
9		.39	.44	0.04	0.01																			.11	.02
10			.32	.58	.04																			.06	.01
11				.27	.50	0.17	0.01																	.04	.02
12					.24	.55	.12																	.04	.04
13						.17	.50	0.21																.11	.02
14							.20	.53	0.19															.05	.02
15								.12	.59	0.22	0.01													.02	.03
16									.12	.54	.18													.09	.07
17										.11	.56	0.23												.06	.03
18											.08	.52	0.23	0.04										.08	.06
19												.03	.50	.16	0.03									.09	.19
20													.04	.54	.27									.00	.15
21														.07	.57	0.29								.00	.07
22															.12	.12	0.38	0.12						.00	.25
23																	.67	.22						.00	.11
24																	.17	.33	0.33					.00	.17
25																			.67	0.33				.00	.00
26																				.50	0.00	0.17		.17	.17
27																					.00	.40	0.00	.40	.20
28																						.50	0.50	.00	.00
29																						.25	.50	.25	.00
>29																								1.0	.00
M[1]																								1.0	.00
C[1]																									1.0

[1] M = dead trees; C = harvested trees.

Table 3. — *Two-step transition probabilities (found by squaring the matrix of table 2)*

Diameter class: at measurement 1 (inches)	Diameter class at measurement 19 (inches)																							M[1]	C[1]
	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	>29		
8	0.14	0.36	0.24	0.05	0.01																			0.18	0.03
9		.15	.31	.28	.04	0.01																		.18	.03
10			.10	.34	.31	.12	0.01																	.10	.02
11				.07	.26	.35	.15	0.04																.09	.05
12					.06	.23	.32	.18	0.02															.12	.07
13						.03	.18	.32	.22	0.05														.16	.04
14							.04	.17	.38	.22	0.04													.09	.06
15								.01	.14	.37	.23	0.06												.10	.09
16									.01	.12	.34	.22	0.04											.15	.10
17										.01	.10	.32	.25	0.06	0.01									.13	.11
18											.01	.06	.29	.21	.10	0.01								.13	.20
19													.03	.29	.23	.05	0.01							.10	.29
20														.06	.35	.19	.10	0.03						.00	.27
21														.01	.11	.09	.40	.13						.00	.25
22															.02	.02	.19	.17	0.21	0.04				.00	.36
23																	.11	.22	.37	.07				.00	.22
24																	.03	.06	.28	.28	0.00	0.06		.06	.25
25																				.33	.00	.24		.24	.18
26																					.00	.24	0.08	.41	.27
27																					.00	.10	.20	.50	.20
28																						.12	.25	.62	.00
29																						.06	.12	.81	.00
>29																								1.0	.00
M[1]																								1.0	.00
C[1]																									1.0

[1] M = dead trees; C = harvested trees.

where $t_j^{(2)}$ is the number of trees in state j after two transitions, regardless of the initial state.

If the values obtained from Equation (10) are defined in vector form as
$t^{(2)} = (t_8^{(2)}, t_9^{(2)}, \ldots, t_{29}^{(2)}, t > 29^{(2)}, t_m^{(2)}, t_c^{(2)})$, then the equation
$t^{(2)} = t^{(0)} \cdot p^{(2)}$
may be used to obtain the individual elements.

The elements $t_m^{(2)}$ and $t_c^{(2)}$ of $t^{(2)}$ are equivalent to the $\Sigma_i m_i$ and $\Sigma_i c_i$ from Equations (7) and (8), respectively. The total number of surviving trees equals
$\sum_i s_i = \sum_i t_i^{(2)}$ for $i = 8 \ldots 29, > 29$.
Thus, this value may be determined as the sum of the elements from Equation (9) or from the sum of all elements of the vector $t^{(2)}$ except death and harvest.

The foregoing relations may be utilized to predict diameter distributions. We demonstrated the predictive ability of the model by using data collected from a stand for 19 consecutive years (table 4). The observed and predicted values agree closely; however, the number of surviving trees by initial diameter class is more accurately predicted than the distribution of surviving trees (Bruner and Moser 1973).

In another study (Cassell and Moser 1974) the trees were grouped into six tolerance classes and each class was individually modeled to provide information on species composition and diameter distribution (tables 5 and 6). The results from this study are similar to those of the composite model. In general the predicted number of surviving trees by species group was accurate and the prediction of death, harvest, and future diameter distribution somewhat less accurate.

For both of the above studies, the basic data were utilized to develop additional models with transition periods of 4, 5, 6, 7, and 8 years. Predictions obtained with these models were similar to those of the 9-year model. Further, it was indicated that the accuracy of prediction was not dependent upon the length of the prediction period but that predictions beyond one period were less accurate.

To utilize the Markov process, the Markov and stationarity properties must be satisfied. First, to predict the next state the present state must be known. Second, the transition probabilities between two specific states must remain constant. In regard to the dynamics of diameter distributions, these properties imply that: (1) the diameter distribution some time in the future

Table 4. — *Observed and predicted stand values at measurement 19 using composite model*
(In number of trees)

d.b.h. class (inches)	Initial no. trees	Survivors		Diameter Distribution		Mortality		Harvested	
		Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted
8	209	175	165	22	28	29	37	5	6
9	148	117	117	97	98	23	26	8	5
10	139	122	122	116	109	15	14	2	3
11	131	110	113	116	108	14	12	7	6
12	111	91	90	94	91	10	14	10	8
13	107	85	86	72	92	14	17	8	4
14	88	76	75	85	79	7	8	5	5
15	86	73	70	74	75	4	8	9	7
16	74	54	55	75	73	8	11	12	8
17	64	50	48	67	66	8	9	6	7
18	52	35	35	67	56	6	7	11	10
19	32	19	20	51	45	3	3	10	9
20	26	19	19	24	35	1	0	6	7
21	14	11	11	36	26	1	0	2	3
22	8	5	5	16	24	0	0	3	3
23	9	5	7	18	8	0	0	4	2
24	6	3	4	7	11	1	0	2	2
25	3	3	2	8	7	0	1	0	1
26	6	3	2	2	7	1	2	2	2
27	5	2	2	7	4	2	3	1	1
28	4	1	2	2	0	2	3	1	0
29	4	3	1	0	4	1	3	0	0
> 29	1	0	0	6	3	1	1	0	0
Totals	1,327	1,062	1,051	1,062	1,049	151	179	114	98

Table 5. — *Observed and predicted survivor distributions at measurement 19 using tolerance class model*
(In number of trees)

d.b.h. class (inches)	Composite distributions			Final distributions											
				Class 1		Class 2		Class 3		Class 4		Class 5		Class 6	
	Initial	Final	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted	Actual	Predicted
8	209	22	29	1	1	1	4	18	23	1	1	0	0	1	1
9	148	97	99	5	7	13	12	75	76	2	2	0	0	2	2
10	139	116	110	3	6	17	18	85	83	7	1	0	0	4	2
11	131	116	111	12	9	21	27	76	66	3	4	0	0	4	5
12	111	94	90	7	4	24	22	54	50	8	10	0	0	1	4
13	107	72	92	4	4	15	17	44	63	8	5	0	0	1	1
14	88	85	80	5	4	[illegible]	10	61	56	6	[illegible]	1	0	3	1
15	86	74	76	3	7	16	13	47	49	5	4	0	0	3	3
16	74	75	71	6	5	11	10	52	50	3	2	0	0	3	3
17	64	67	68	5	2	9	13	46	45	4	3	0	0	3	5
18	52	67	56	3	5	12	7	41	39	6	3	0	0	5	1
19	32	51	46	5	4	5	7	36	30	4	2	0	0	1	2
20	26	24	36	1	3	3	5	20	27	0	0	0	0	0	2
21	14	36	24	3	1	4	2	28	20	0	0	0	0	1	1
22	8	16	26	0	0	2	1	14	23	0	0	0	0	0	1
23	9	18	9	0	1	1	2	15	6	0	0	0	0	2	1
24	6	7	11	0	1	1	1	6	9	0	0	0	0	0	0
25	3	8	6	1	0	0	2	7	5	0	0	0	0	0	0
26	6	2	7	0	0	0	1	2	6	0	0	0	0	0	1
27	5	7	4	0	0	0	0	6	4	0	0	0	0	1	1
28	4	2	0	0	0	0	0	2	0	0	0	0	0	0	0
29	4	0	6	0	0	0	0	0	6	0	0	0	0	0	0
> 29	1	6	5	0	0	3	4	2	0	0	0	0	0	1	1
Totals	1,327	1,062	1,062	64	64	167	178	737	736	57	46	1	0	36	38

Table 6. — *Observed and predicted mortality and harvest at measurement 19 using tolerance class model*
(In number of trees)

Class	Measurement 19			
	Mortality		Harvested	
	Actual	Predicted	Actual	Predicted
1	0	1	0	0
2	16	7	13	9
3	31	44	50	38
4	9	19	2	4
5	0	1	0	0
6	1	0	1	1
Totals	57	72	66	52

depends only upon the distribution now and not upon past distributions; and (2) the probability of a tree moving, for instance, from the 8-inch to the 9-inch class in any specific period must remain the same regardless of stand conditions.

The larger discrepancies for predictions beyond one period may be attributable to not satisfying the stationarity assumption. To examine this possibility, the 19 years of remeasurement data were used to determine transition probabilities between the various states over time. These probabilities were fairly constant for diameter classes with a large initial number of trees, but this was not true for diameter classes with a small initial number of trees. This suggests that the accuracy of predictions for several periods is dependent upon good estimates of the transition probabilities which, in turn, are dependent upon sufficient data for all diameter classes. Also, because uneven-aged stands are characterized by a large number of trees in the lower diameter classes, permanent plot data from such stands will have a similar diameter distribution. This situation will inherently lead to greater accuracy in prediction in the lower classes.

Prediction of diameter distributions with the Markov model has both positive and negative points. One disadvantage is that mortality and harvested trees are predicted as numbers of trees by original diameter class so that the actual diameter class of a tree when it dies or is harvested is not known. Another disadvantage is the difficulty of introducing ingrowth into the process. The only way to allow for ingrowth is to inventory trees in diameter classes below the lower limit for which predictions are important. For example, if predictions with ingrowth are desired for sawtimber trees in the 12-inch diameter classes and above, trees in the 8-, 9-, 10-, and 11-inch diameter classes at the initial measurement can be considered as possible ingrowth into the 12-inch and larger classes during the prediction periods. To include ingrowth in all diameter classes 8 inches and above, trees in roughly the 4-, 5-, 6-, and 7-inch diameter classes would have be inventoried. A third disadvantage is the lack of flexibility in the length of prediction periods. If the two inventory measurements used for the prediction are, for example, 5 years apart, predictions of stand conditions can only be made for subsequent multiples of 5 years. Lastly, at least two measurements from permanent plots are required as data for predictions. This prediction method is not applicable for areas not under a continuous forest inventory system.

Ease of application is a major benefit of the Markov model. Accurate predictions of numbers of survivor, dead, and harvested trees, and the distribution of surviving trees depend only upon conventional continuous forest inventory data and a knowledge of elementary matrix operations.

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AN ACCURATE WAY TO SELECT SAMPLE PLOTS ON AERIAL PHOTOS USING GROUND CONTROL

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Most forest inventories begin with the classification of points selected from individual aerial photographs. The information developed from this procedure is subject to several sources of error. Photo cover type classification of a sample point can be in error due to the quality and age of the photos or to the skill of the photo interpreter. These errors can be adjusted by field checking a portion of the photo points. A source of error that cannot be corrected by field checking occurs when end lap (overlap), sidelap, crab, and tilt distort the photo coverage of the land area. This results in some areas being sampled more intensively than others.

The normal forest aerial photography contracts specifies 60 percent endlap and 30 percent sidelap in line of flight. However, the contractor usually delivers more coverage of the area to be sure that these requirements are met. This type of bias is recognized by aerial photo interpreters, but usually ignored in the hope that the errors will be compensating. Contract specifications for aerial photos also require a specific scale — the deviation from specified flight altitudes shall not exceed 300 feet for the purchaser to accept the photos.

We tested photo intensity during the forest survey in Iowa where photographing conditions were good — differences in elevation were moderate and each township had many roads lying north-south and east-west. In spite of these ideal conditions, photo overlap was 0.66 percent greater than specified, which represented 237,000 acres. This means that in sampling individual photos, without regard to overlap variation, area of the predominant land class would have been overestimated. A similar test done by the Pacific Northwest Forest and Range Experiment Station in Oregon and Washington had similar results (Pope *et al.* 1972).

PROCEDURES USED AT OTHER STATIONS

The PNW selects plot locations on maps, then transfers these plot locations to aerial photos using a radial line plotter or stereopotter. This procedure is considered too expensive by many inventory foresters.

The Southern Forest Experiment Station locates sample plots on the most recent conventional aerial photographs and establishes them on the ground. Then assigns geographic coordinates to the nearest mile for each plot using a coordinatograph with a 7½-minute quadrangle. The cost of this method is considered rather high also.

The Southern Region establishes forest survey field plots on maps by a systematic grid. Then transfers these locations to aerial photos and establishes a cluster of photo plots on each photo containing a field plot.

The Northeastern Region locates samples directly on individual conventional photos. Then arranges samples systematically using three photo plots per photo print and randomly chooses ground plots by photo class.

A new way was needed to use these photos that would estimate forest area accurately. Forest Survey at the North Central Station approached the problem with the objectives to: (1) select plot locations on aerial photos that would avoid bias due to uneven photo intensity, (2) determine how to select the proper grid scale to represent the land area sampled, and (3) keep costs down. The method we developed is described below.

NORTH CENTRAL PROCEDURE

A township mosaic is assembled from individual conventional photos for each township in our Region instead of using single individual conventional photos. Next, township boundaries are transferred from maps of plat books to the mosaic (thus providing the gound control of the area). This compensates for overlap, sidelap, crab (apparent sidewise motion of an airplane headed into a cross-wind), and tilt (departure from the vertical position of the camera). The time spent to assemble one township is ½ to 1 hour. Then a systematic grid of plots is placed over the township mosiac. Therefore, sample plots are uniformly spaced and an equal number of plots is represented in each township.

In our Region differences in relief are not great and contracting companies usually deliver photos in the prescribed range, but the scale of photos varies. To compensate for this, we have many sets of grids with variations of scale from 1:15,000 to 1:42,000. The appropriate grid is selected to match the scale of the photo mosaic.

The township mosaic assembly corresponds closely to township area on the ground. To avoid too many of the plots falling on roads (north-south and east-west), the grid is turned 5 degrees to the left. In the eastern part of the United States where land area is not divided by the township and range system, other controls of land area could be used such as geological survey contour maps (U.S.G.S. quads).

RESULTS AND DISCUSSION

The assembled mosaic system allows us to locate plots systematically on the aerial photos, which minimizes the bias due to photography in photo plot sampling. We still cannot entirely eliminate small differences of relief and some distortion on the edge of the photos, but we do eliminate costs of the map-ground transfer process and believe that our statistical results are realistic.

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ESTIMATING D.B.H. FROM STUMP DIMENSIONS

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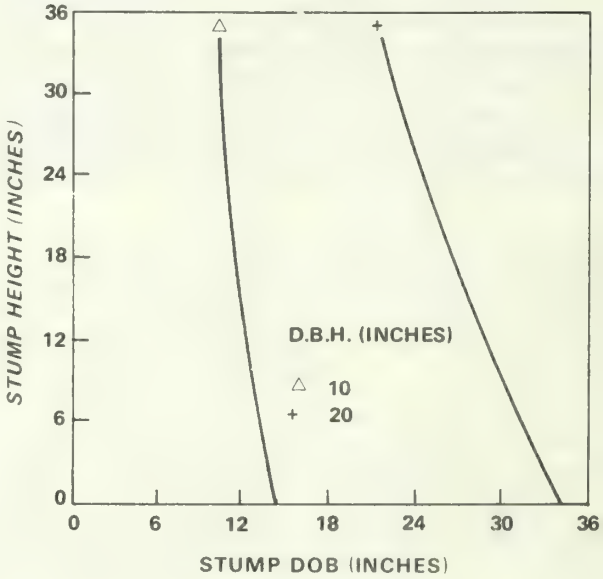
A means of estimating diameter at breast height (d.b.h.) from stump measurements has several applications: (1) the volume removed in cases of timber tresspass can be calculated using local volume tables, (2) diameter distributions and basal areas for sample plots or stands can be calculated if trees have been cut and the data were not previously recorded or were lost, and (3) removals from a large forest area can be calculated. The equations presented here were developed as part of the 1977 Minnesota forest inventory. The d.b.h. estimated by these equations was used as an input to other volume equations to make an estimate of the timber removed from Minnesota's forests.

Previous studies of d.b.h. and stump diameter relations in other regions of the country have included few tree species of interest in the north-central States or have not been done in a form easily adaptable to forest inventory computer processing. Several of these studies were published only as tables or charts (Rapraeger 1941, Cunningham *et al.* 1947), while others were based on a linear relation from a fixed stump height (Bones 1960, 1961). Stump height was used as a variable by Curtis and Arney (1977) for estimating d.b.h. of second-growth Douglas-fir in the Pacific Northwest. McClure (1968) used stump height in a model similar to the model used in our study but his equations and tables cover species found in the southeast.

METHODS

We collected data from 2,575 trees. These data were collected as part of forest product utilization studies conducted in conjunction with forest inventories in Michigan, Wisconsin, and Minnesota. Measurements were taken from random samples of felled trees at logging operations in these States. Along with the d.b.h. for each tree, the diameter outside bark (d.o.b.) was measured to the nearest 0.1 inch at half-foot intervals from 0.5 to 2.5 feet above the ground (table 1). If an abnormality, such as a bulge or fork, occured at the measurement height, the measurement was not taken.

Table 1. — *D.b.h. regression coefficients for tree species of the Lake States*



RESULTS

Because the best estimate of d.b.h. is obtained by measuring stump diameter at the highest point on a given stump and stump heights vary so greatly, stump height was chosen as an independent variable along with d.o.b. Plotting the ratios of d.b.h. to d.o.b. suggests a model of the form:

$$\frac{\text{d.b.h.}}{\text{d.o.b.}} = A + B \cdot \ln(H) + C \cdot \text{d.o.b.} \cdot H$$

where, A,B, & C = regression parameters, and H = stump height at which d.o.b. was measured.

Then, we modified the equation as follows to make it usable for stump heights ranging from 0 to 4.5 feet, because the natural logarithm of zero is undefined.

$$\frac{\text{d.b.h.}}{\text{d.o.b.}} -1 + A + B \cdot (\ln(H + 1.0) = \ln \cdot 5.5) + C \cdot \text{d.o.b.} \cdot (H-4.5)$$

where, A = the regression coefficient for a given species group, B + C = regression coefficients, H = stump height in feet, d.o.b. = stump diameter outside bark in inches at H, and d.b.h. = diameter at breast height in inches.

This modified regression model was fit using multiple linear regression with species groups as a dummy variable. The species included in each species group are listed below.

Common name	Scientific name
SOFTWOODS	
Eastern white pine	*Pinus strobus*
Red pine	*Pinus resinosa*
Jack pine	*Pinus banksiana*
White spruce	*Picea glauca*
Black spruce	*Picea mariana*
Balsam fir	*Abies balsamea* var. *balsamea*
Tamarack	*Larix laricina*
Northern white-cedar	*Thuja occidentalis*
Other softwoods	*Juniperus virginiana* all other softwoods
HARDWOODS	
Oaks	*Quercus alba* *Quercus bicolor* *Quercus macrocarpa*
Red oak	*Quercus rubra*
Northern pin oak	*Quercus ellipsoidalis*
Hickories	*Carya cordiformis* *Carya ovata*
Yellow birch	*Betula alleghaniensis*
Hard maples	*Acer nigrum* *Acer saccharum*
Soft maples	*Acer rubrum* var. *rubrum* *Acer saccharinum*
Ashes	*Fraxinus americana* *Fraxinus nigra* *Fraxinus pennsylvanica*
Balsam poplar	*Populus balsamifera*
Paper birch	*Betula papyrifera* var. *papyrifera*
Bigtooth aspen	*Populus grandidentata*
Quaking aspen	*Populus tremuloides*
American basswood	*Tilia americana*
Elms	*Ulmus americana* *Ulmus rubra* *Ulmus thomassii*
Select hardwoods	*Juglans cinerea* *Juglans nigra* *Prunus serotina*
Other hardwoods	*Acer negundo* *Betula nigra* *Celtis occidentalis* *Populus deltoides*
Noncommercial species	

The R^2 for the regression is 0.64616 and the standard error of estimate is 0.5955. The A + 1 coefficients B and C equal 0.1273 and 0.001641, respectively.

Figure 1 illustrates the advantages of this model, which increases the taper in the lower section of the stump for large trees. For examples, the data for northern white-cedar, balsam poplar and bigtooth aspen, and ash have been put in table form (tables 2, 3, and 4). These tables may be used to find the estimated d.b.h.'s for these trees when the stump height and stump d.o.b. are known. When the stump diameter is in other than 1-inch increments, interpolate to estimate d.b.h. A graph could be used in the field as a quick method of estimating d.b.h. (fig.2).

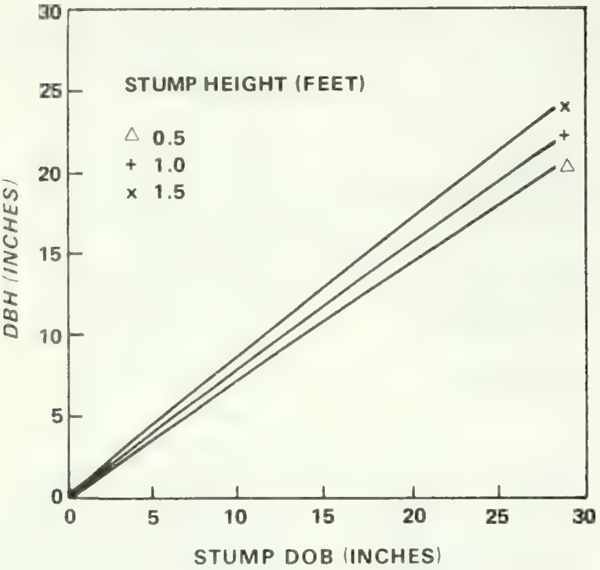


Figure 1. — *The relation of stump height and stump d.o.b. for 10- and 20-inch d.b.h. red pine.*

Species group	Trees	Observations	D.b.h. range	Coefficient A + 1.0
	Number		*Inches*	
White pine	34	138	9.4-33.0	1.07035
Red pine	98	392	3.4-22.6	1.05462
Jack pine	474	1918	4.9-19.4	1.04608
White spruce	51	117	5.0-18.4	1.01082
Black spruce	124	426	5.0-13.3	1.02679
Balsam fir	189	532	4.2-15.6	1.01367
Tamarack	7	14	7.2-9.2	1.01752
Northern white-cedar	97	194	5.2-17.2	.95610
Other softwoods	--	--	--	[1]1.04608
White oak	34	137	10.6-22.9	1.04427
Red & northern pin oak	107	425	6.3-30.6	1.05658
Hickory	--	--	--	[2]1.05658
Yellow birch	22	47	13.2-23.8	1.10481
Hard maple	89	239	5.7-24.2	1.05199
Soft maple	27	114	8.0-24.2	1.05199
Ash	31	218	7.4-24.7	1.05559
Balsam poplar, Bigtooth aspen	187	582	5.0-17.8	1.07897
Paper birch	189	795	5.0-13.8	1.05155
Quaking aspen	738	2706	5.0-20.5	1.06439
Basswood	25	99	9.8-26.7	1.07428
Elm	48	174	7.0-30.5	1.06734
Select hardwoods	4	20	8.1-11.7	1.10929
Other hardwoods	--	--	--	[3]1.06439
Noncommercial species	--	--	--	[3]1.06439
TOTAL	2,575	9,287	3.4-33.0	--

[1] Used the value for jack pine.
[2] Used the value for red oak.
[3] Used the value for quaking aspen.

Figure 2. — *D.b.h. for red pine as a function of stump d.o.b.*

Table 2. — *Estimated d.b.h. for northern white-cedar from stump height and d.o.b.*
(In inches)

Stump d.o.b.	Stump height (feet) 0.5	1.0	1.5	2.0
5	3.8	4.0	4.2	4.3
6	4.5	4.8	5.0	5.1
7	5.2	5.5	5.7	6.0
8	5.9	6.3	6.5	6.8
9	6.6	7.0	7.3	7.6
10	7.3	7.7	8.1	8.4
11	7.9	8.4	8.8	9.2
12	8.5	9.1	9.6	10.0
13	9.2	9.8	10.3	10.7
14	9.8	10.5	11.0	11.5
15	10.4	11.1	11.7	12.3
16	11.0	11.8	12.4	13.0
17	11.5	12.4	13.1	13.8
18	12.1	13.0	13.8	14.5
19	12.7	13.6	14.5	15.2
20	13.2	14.2	15.1	15.9
21	13.7	14.8	15.8	16.6
22	14.2	15.4	16.4	17.4
23	14.7	16.0	17.1	18.0
24	15.2	16.5	17.7	18.7
25	15.7	17.1	18.3	19.4
26	16.1	17.6	18.9	20.1
27	16.6	18.2	19.5	20.7
28	17.0	18.7	20.1	21.4
29	17.4	19.2	20.7	22.0
30	17.8	19.7	21.2	22.7
31	18.2	20.1	21.8	23.3
32	18.6	20.6	22.3	23.9
33	18.9	21.0	22.9	24.5
34	19.3	21.5	23.4	25.1
35	19.6	21.9	23.9	25.7
36	20.0	22.3	24.4	26.3

Table 3. — *Estimated d.b.h. for bigtooth aspen and balsam poplar from stump height and d.o.b.* (In inches)

Stump d.o.b.	Stump height (feet) 0.5	1.0	1.5	2.0
5	4.4	4.6	4.8	4.9
6	5.2	5.5	5.7	5.9
7	6.1	6.4	6.6	6.8
8	6.9	7.2	7.5	7.8
9	7.7	8.1	8.4	8.7
10	8.5	8.9	9.3	9.6
11	9.3	9.8	10.2	10.5
12	10.0	10.6	11.0	11.4
13	10.8	11.4	11.9	12.3
14	11.5	12.2	12.7	13.2
15	12.2	13.0	13.6	14.1
16	12.9	13.7	14.4	15.0
17	13.6	14.5	15.2	15.8
18	14.3	15.2	16.0	16.7
19	15.0	16.0	16.8	17.6
20	15.6	16.7	17.6	18.4
21	16.3	17.4	18.4	19.2
22	16.9	18.1	19.1	20.1
23	17.5	18.8	19.9	20.9
24	18.1	19.5	20.7	21.7
25	18.7	20.2	21.4	22.5
26	19.3	20.8	22.1	23.3
27	19.9	21.5	22.8	24.1
28	20.4	22.1	23.5	24.8
29	21.0	22.7	24.2	25.6
30	21.5	23.3	24.9	26.4
31	22.0	23.9	25.6	27.1
32	22.5	24.5	26.3	27.9
33	23.0	25.1	26.9	28.6
34	23.5	25.7	27.6	29.3
35	23.9	26.2	28.2	30.0
36	24.4	26.8	28.8	30.7

Table 4. — *Estimated d.b.h. for ash from stump height and d.o.b.* (In inches)

Stump d.o.b.	Stump height (feet) 0.5	1.0	1.5	2.0
5	4.3	4.5	4.7	4.8
6	5.1	5.4	5.6	5.7
7	5.9	6.2	6.4	6.6
8	6.7	7.0	7.3	7.6
9	7.5	7.9	8.2	8.5
10	8.2	8.7	9.1	9.4
11	9.0	9.5	9.9	10.3
12	9.7	10.3	10.8	11.2
13	10.5	11.1	11.6	12.0
14	11.2	11.8	12.4	12.9
15	11.9	12.6	13.2	13.8
16	12.6	13.4	14.0	14.6
17	13.2	14.1	14.8	15.4
18	13.9	14.8	15.6	16.3
19	14.5	15.5	16.4	17.1
20	15.2	16.2	17.1	17.9
21	15.8	16.9	17.9	18.7
22	16.4	17.6	18.6	19.5
23	17.0	18.3	19.4	20.3
24	17.6	18.9	20.1	21.1
25	18.2	19.6	20.8	21.9
26	18.7	20.2	21.5	22.7
27	19.3	20.8	22.2	23.4
28	19.8	21.4	22.9	24.2
29	20.3	22.0	23.6	24.9
30	20.8	22.6	24.2	25.7
31	21.3	23.2	24.9	26.4
32	21.8	23.8	25.5	27.1
33	22.2	24.3	26.2	27.8
34	22.7	24.9	26.8	28.5
35	23.1	25.4	27.4	29.2
36	23.5	25.9	28.0	29.9

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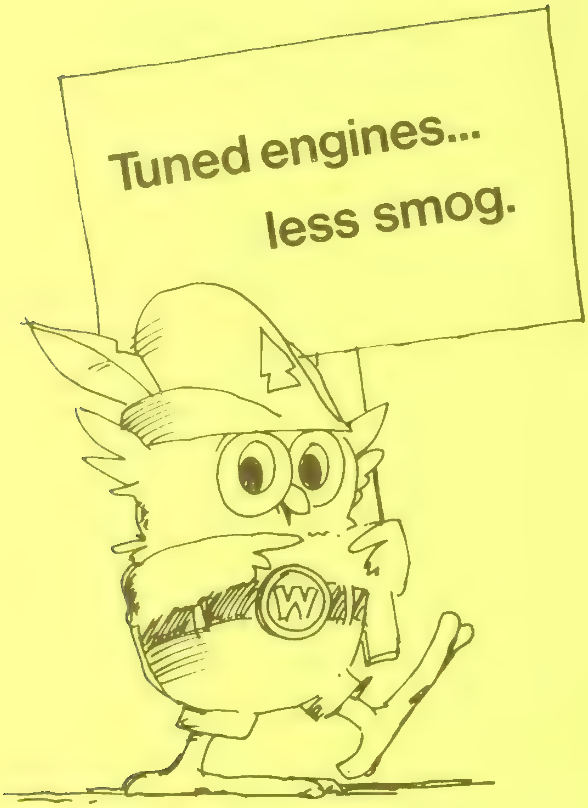
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SOME HARVEST OPTIONS AND THEIR CONSEQUENCES FOR THE ASPEN, BIRCH, AND ASSOCIATED CONIFER FOREST TYPES OF THE LAKE STATES

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D.C. Lothner, D.A. Perala,
A.L. Schipper,Jr., and E.S. Verry

Aspen
Birch
Conifer
PROGRAM REPORT

th Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture

This paper is a contribution from the Aspen-Birch-Conifer Program. The Aspen-Birch-Conifer Program is a coordinated, multidisciplinary research effort. Its mission is to increase and integrate knowledge of the aspen-birch-conifer forests of the northern Great Lakes region in order to better identify and evaluate resource management alternatives.

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SOME HARVEST OPTIONS AND THEIR CONSEQUENCES FOR THE ASPEN, BIRCH, AND ASSOCIATED CONIFER FOREST TYPES OF THE LAKE STATES

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INTRODUCTION

National needs for timber are increasing, along with demands for other uses of forest land. To meet these demands, many forest landowners and managers are attempting to increase wood production and at the same time provide wildlife, water, and recreational opportunities. Public land managers are legally committed to the multiple-use principle, and private owners usually find it to their advantage to manage their land for several resources. Thus, almost all forest landowners face the problem of a limited land base and multiple demands for the resources it can produce. As a consequence, difficult management choices must be made and the trade-offs carefully evaluated, because any change in the management of one resource will invariably affect the others.

This paper focuses on harvest options for eight important forest types of the northern Lake States: aspen, white birch, red pine, white pine, jack pine, black spruce, spruce-fir, and northern white-cedar. It is intended to help landowners and managers identify some recommended harvest options and to aid them in evaluating the consequences (trade-offs) of each. Once a harvest option is decided on, several sources can be consulted for details on *how* to harvest and regenerate specific forest types. For example:

1. Manager's Handbooks are newly available for six of the forest types covered in this paper: aspen (Perala 1977), white birch (Tubbs 1977), jack pine (Benzie 1977a), red pine (Benzie 1977b), black spruce (Johnston 1977a), and northern white-cedar (Johnston 1977b). They can be obtained free of charge from the North Central Forest Experiment Station, 1992 Folwell Avenue, St. Paul, Minnesota 55108.

2. More detailed information for the white birch and spruce-fir forest types is available in management guides published earlier (Marquis *et al.* 1969

and Frank and Bjorkbom 1973, respectively). These guides are based on conditions in the northeastern United States, thus not all the recommendations are applicable to the Lake States. They can be obtained from the Northeastern Forest Experiment Station, 370 Reed Road, Broomall, Pennsylvania 19008.

3. Additional information for the white pine type is available in USDA Handbook No. 445 (Little *et al.* 1973), which can be obtained from the Superintendent of Documents, U.S. Government Printing Office, Washington, D.C. 20402 (Price $0.80 domestic postpaid).

4. Specific management information and operating plans are available from private consultants or state extension foresters.

AREA OF APPLICATION

The harvest options and evaluations apply to the aspen, white birch, and associated conifer forest types of Michigan, Minnesota, and Wisconsin. These forests are most prevalent in Upper Michigan and the northern half of Lower Michigan, northeastern and north-central Minnesota, and northern Wisconsin (fig. 1).

The forest types described occupy 27.1 million acres, or 54 percent of the total commercial forest land in the Lake States. Forty-one percent (11.2 million acres) of the area occupied by these types occurs in Minnesota, 34 percent (9.1 million acres) in Michigan, and 25 percent (6.8 million acres) in Wisconsin.

These lands were glaciated during the Wisconsin glacial stage of the Pleistocene epoch. Soils include glacial till, outwash sands and gravels, and organic accumulations in lowlands. They range from poorly drained depressions and peatlands to droughty sands and gravels, and support a large variety of plants and animals. Terrain is flat to gently rolling with occasional outcrop ridges and numerous lakes and streams.

The growth potential of these stands is generally much greater than that currently being

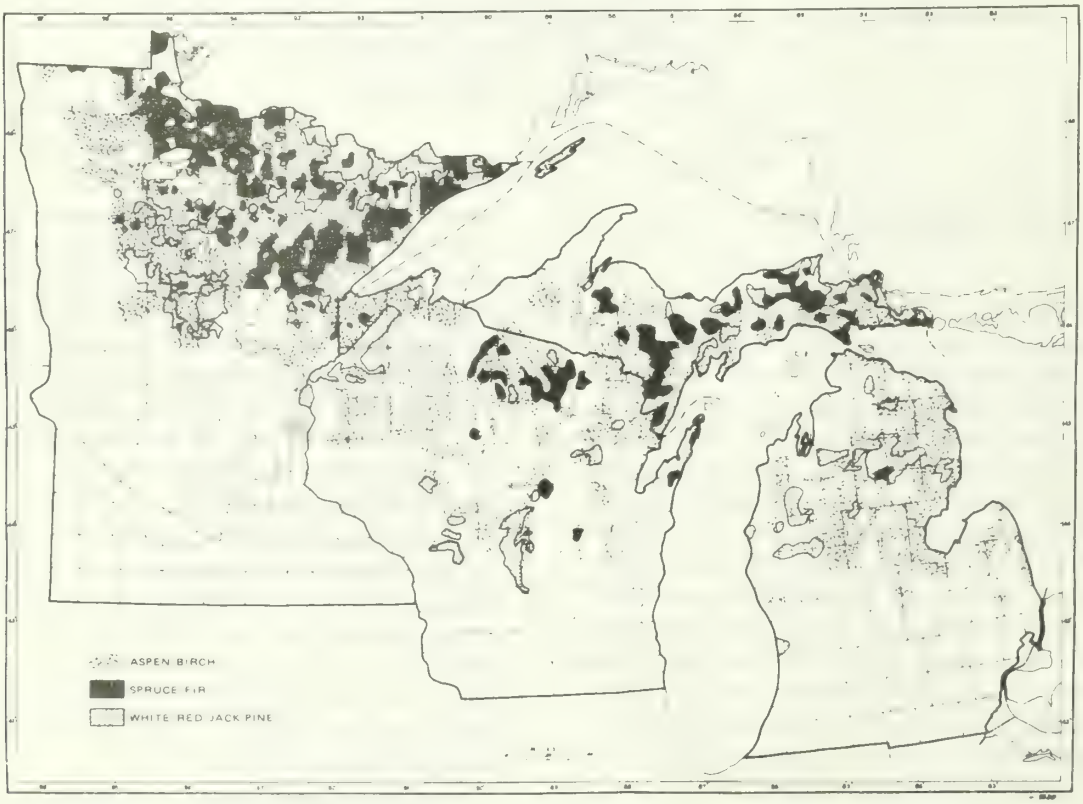

Figure 1.—*Distribution of the aspen-birch, spruce-fir, and white-red-jack pine forest types in Michigan, Minnesota, and Wisconsin. Information from Forest Service Survey data.*

achieved. Growth could be increased markedly by using more intensive silvicultural practices such as thinning, by conversion to faster-growing species, by planting genetically superior seedlings, and possibly by fertilization and irrigation.

RATIONALE FOR HARVEST OPTION RATINGS

Harvest options were rated by evaluating the effects of three common mangement practices on timber investment return, water, wildlife, and visual quality. The practices considered were (1) even-aged management, (2) uneven-aged management, periodic harvesting the same stand of selected trees of different ages, and (3) no management allowing stands to mature, die, and regenerate new stands of the same or different species according to successional trends without harvesting.

The basic information considered in our ratings is summarized below for each resource.

Timber

Lumbering of white pine and red pine sawtimber began about 100 years ago in the Lake States, reaching a peak at the turn of the century. Because of inadequate provision for regeneration and the widespread fires that followed logging, the land once dominated by these pines was converted largely to aspen. Once considered a weed tree, aspen is now the mainstay of a large pulp and paper industry. Thus, although sawtimber production today is less than pulpwood production, the aspen, birch, and associated conifer forest types have contributed significantly to the region's timber needs. Approximately 62 percent of the total Lake States timber harvest is derived from these forest types, although they occupy only 54 percent of the commercial forest land. Aspen and jack pine rate first and second in overall utilization. In terms of value per unit area cut, however, red pine still ranks as the number one species.

Most of the eight forest types are dominated by shade-intolerant species characteristic of early forest succession, and thus lend themselves best to even-aged silvicultural systems. Even-aged management can be simply a clearcut operation at rotation age followed by natural or artificial reproduction, as is commonly done with jack pine, or it can be reproduction through resprouting, as is common in aspen. It can also include a series of thinnings as the stand matures, or sometimes a shelterwood cut near the end of the rotation to provide natural regeneration, followed by removal of shelterwood trees after stand establishment, as is practiced for red pine in parts of the Lake States. Only the spruce-fir forest type, and in some portions of the region, the white pine and northern white-cedar types, can be managed under uneven-aged silvicultural systems. Uneven-aged systems do not provide satisfactory seedbed conditions or adequate light for regenerating and growing most of the eight forest types.

Even-aged silvicultural practices vary from extensive management characterized by a "let-grow" philosophy to more intensive management, including both noncommercial and commercial thinnings prior to final harvest. The intensity of management depends on species composition, stand condition, site quality, markets, and owner objectives. In addition to these constraints and the limitations imposed by management for other resources, our ratings have assumed the best possible implementation of silvicultural practices.

The rating scheme for timber is based on an objective of maximizing investment returns within the different management systems and product objectives. We have assumed an average site, although we recognize that investment returns are greater for timber management on the better sites.

The following general relations formed the basis for the ratings:

1. Larger clearcuts are more profitable than smaller ones, within the range we are considering (economy of scale).
2. Where a variety of product markets are available, multi-product objectives (sawtimber, veneer, pulpwood) are more profitable than single-product objectives.
3. With shade-intolerant species, regeneration is more successful when clearcuts are large enough for full light penetration.
4. For a given product objective, shorter rotations provide higher rates of return on investment. However, landowners and managers

should be aware that even when timber stands are held past optimum financial rotation by 10 to 20 years, loss on rate of return is often minimal.

Water

Supplies of high-quality water are adequate in northern Lake States forests during years of normal precipitation. Such years have about 30 inches of rain and snow and produce about 10 inches of water yield (either streamflow, ground water recharge, or both). Spring flooding usually occurs in years with deep snowpacks, especially when warm spring rains fall on top of the snow. But local flooding can also occur during the warm season when rainfall exceeds 10 inches per month. Long droughts also occur, drying up wetlands and lowering ground water levels. Climate, rather than land management activity, is the major regulator of ground water recharge and streamflow. It alone can account for variations in annual streamflow on the order of −75 to +250 percent of the mean.

There are basically two ways that forest management can affect water yield. First, harvesting the trees can increase streamflow as much as 60 percent the first year after cutting. The amount diminishes over time, but 7 to 10 years may elapse before streamflow returns to the pre-cut level. Annual streamflow peaks (spring flood peaks) may double if the harvested area covers an entire watershed. However, most timber harvests cover only a fraction of a watershed; also, snowmelt occurs earlier in harvested areas than in surrounding areas, tending to reduce peak flows (Verry 1972).

Second, conversion from hardwood to pine can reduce annual streamflow, because pine trees intercept and evaporate about 2.6 inches more of the annual precipitation than do hardwoods. This effect lasts throughout the rotation once crown closure is complete. In addition, pines transpire more water than hardwoods on an annual basis. In wet areas where evapotranspiration is at or very near maximum regardless of vegetative cover, species differences are unimportant (Verry 1976, Urie 1977).

Although clearcutting can cause a drastic change in annual streamflow on a small area, it will not have a great impact on the water yield over a large area. For example, on areas of 250,000-plus acres it is unlikely that forest management will affect the annual flow of rivers by more than 5 percent of the mean. The reason is that only about 1 to 3 percent of the commercial forest area is cut in any one year, and the effects of management are thus spread over a long period. The change in streamflow caused by harvesting is greatest the first year and diminishes with time. And most important, the streamflow from large areas is strongly influenced by ground water inflow to the channel. The rate of ground water inflow depends on the climate over several years and thus overrides impacts of land management on small areas.

Current forest management practices in the Lake States do not significantly affect stream sedimentation because of the relatively flat terrain, the high permeability of soils, and logging limitations on Federal lands near shorelines. Where roads must be built on steeper slopes and on soils with high silt and clay content, action can be taken to prevent or control erosion (Kochenderfer 1970). Rapid revegetation of disturbed areas, common in this climatic region, also relieves the erosion and sediment threat of logging.

Clearcutting aspen on uplands does not change the concentration of nutrients in streamflow (Verry 1972) or in ground water (Richardson and Lund 1975). However, clearcutting of brushy black spruce stands on organic soils will increase the concentrations of iron, manganese, magnesium, potassium, and phosphorus in streamflow by about 2½ times when air temperatures exceed 80° F. These increases in nutrient concentrations on small watersheds do not appear to persist more than 0.25 miles downstream, and phosphorus input to lakes is insignificant. Clearcutting nonbrushy, acid bogs does not significantly change nutrient concentrations in streamflow (Verry 1976).

Stream water temperatures increase if trees shading the channel are removed, but water influence zones require modified or restricted logging near shorelines. However, these strips of trees along waterways must be wide enough to prevent windthrow.

Herbicides are used for tree release and occasionally for site preparation in the Lake States. The correct use of herbicides in the forest will not result in a hazard to people or wildlife assuming concentrated solutions are not spilled directly into watercourses (Norris 1975).

Fertilizers have not been widely used in the Lake States forests. Human sewage effluent and sludge application to forest lands is being done on small areas, and preliminary water monitoring indicates that conservative operations do not endanger water supplies. Application of sewage effluent and sludge on forest land appears to offer an economical tertiary treatment except where large amounts of municipal or industrial waste must be handled and limited land resources are expensive.

Wildlife

The diversity of the aspen, birch, and associated conifer forest types is also reflected in the animal communities they support. For example, Peterson (1975) divided the area covered by the North American Breeding Bird Survey into 56 ecological units in which the northern Lake States region is classified as spruce-hardwood forest. By various measures, this unit ranks among the top five in species diversity. Thus, it is evident that the region is highly important to a large variety of birds, even if only seasonally.

The fact that some areas of the region are remote from permanent settlement and are adjacent to Canada has permitted certain carnivores, such as the timber wolf, to maintain viable populations and thus contribute to the unique diversity of the ecosystem.

In early times, interest in the wildlife of the region focused on the furbearers, and later shifted to the game species (especially white-tailed deer, ruffed grouse, and waterfowl). Accordingly, for many years most wildlife programs revolved around the management of these species. Today, however, society is demanding that all wildlife be considered in land management, and herein lies a problem: knowledge of the impact of management activities is generally limited to the game species. Likewise, the greater the species diversity present, the greater the potential for impacts from each management activity, and the greater the potential for conflicting impacts (i.e., what helps one species may harm another).

Limited knowledge of the habitat requirements for most wildlife also poses a problem in evaluating the impact of harvest options. In these cases the ratings reflect our best estimates, and should be considered tentative until confirmed by future knowledge.

To maintain simplicity and yet take into account the variability in habitat requirements of a large number of species, wildlife was divided into two groups called "edge" and "interior" species (Trimble *et al.* 1974). Edge species are those associated with forest edges, openings, shrubs, and ground vegetation. Examples of this group are the white-tailed deer, black bear, ruffed grouse, snowshoe hare, beaver, and a large number of nongame birds and mammals (Appendix Table 2). Interior species are those associated more with the tree layer of maturing and old growth forest communities. Squirrels, marten, and warblers are typical of this group (Appendix Table 2). In general, the majority of both game and nongame species belongs to the edge group.

The most economical means of altering the habitat on large areas is through the use of silvicultural techniques (including fire). With proper planning silvicultural techniques can serve both timber and wildlife objectives. Specific habitat manipulation measures for wildlife, such as creating openings, seeding old roads and trails, and erecting nest structures, were not considered because they can be applied independent of managing land as a timber resource.

The ratings for wildlife assume the following: (1) options that return habitat to younger successional stages or maintain younger age classes (shorter rotations, thinning, etc.) are generally beneficial to edge species, while longer rotations and few intermediate treatments are more beneficial to interior species. (2) In the case of both edge and interior species, options that alter the vegetation of large acreages in a single area are generally undesirable. (3) Harvest units of 1 acre or less are considered less desirable than units approaching 5 acres, since the ratio of the edge to the size of the harvest unit tend to exceed 1.0 for units of 1 acre or less.

However, even with wildlife production as a primary goal, managers could at times and with good reason select options that are rated low here. Each manager needs to assess not only his objectives and the habitats available on his holdings, but also those of other holdings in the surrounding area. This is especially important for wide-ranging wildlife species whose needs transcend ownership boundaries. Small landowners, whose objectives may be based more on amenities than economic considerations, may want to provide habitats that are in short supply locally or create habitat more specific to certain species.

Visual Quality

Throughout the Lake States there is great potential for timber harvest to affect the visual quality of the landscape, both favorably and unfavorably.

Because the forest types are dominated by pioneer tree species that have evolved even-aged structures, the recommended forest management system is to maintain stands of even-aged trees. The harvesting methods under this system increase the potential for imparing visual quality, but can also open vistas and relieve monotonous landscapes.

Because sharp breaks are not common on the regional landscape, major openings created by land management practices may appear unattractive. However, carefully planned timber harvests, if patterned to blend in with the forest landscape, can be visually apppealing.

The forest landowner must recognize that virtually any forest operation that involves timber removal will temporarily affect on-site visual quality. Professional foresters are available to assist landowners in preparing management plans that will provide wood products, improve wildlife habitat, and yet maintain the visual quality of an area. Noyes (1969) suggests the following harvest controls:

1. Utilize all material possible from harvesting operations.
2. Enhance aesthetic qualities by developing vistas and emphasizing desirable topographic features of the area.
3. Protect seedlings and shrubs by careful skidding and hauling procedures.
4. Replace cut trees by planting seedlings, utilizing natural seedlings, or releasing desirable understory stems alreay established.
5. Protect the site against erosion by well-planned skid and haul road layout, and adequate water drainage facilities.
6. Clean up refuse, tin cans, discarded equipment and parts.
7. Cut up logging slash to lie close to the ground following harvest. Slash can also be disposed of by burning, full-tree logging, or full-tree chipping.

In addition to the degree of control during harvest, the recovery period will also depend on the productivity of the site and the post-logging practices to encourage rapid revegetation (Perala 1977).

Visual quality, both distant and close-up, is enhanced by the presence of large trees. Thus, management options that provide for longer rotations less frequent disturbance will improve visual quality.

A diversity of plant species also enhances visual quality. We considered a forest practice to have a positive influence on the landscape if it (slightly modified from Trimble, *et al.* (1974)):

1. Affects only a relatively small forest area.
2. Complements the shape and form of natural forest openings.
3. Favors rapid vegetative regeneration and growth.
4. Allows larger trees to occupy the site for long periods.
5. Allows for maximum time between cuttings so that forest cover will occupy the site as long as possible.
6. Minimizes physical site damage.
7. Occurs on more fertile sites.

METHOD OF PRESENTATION

We have presented harvest options and information in three forms.

First, we rated each of the forest types according to its production potential for timber, water, wildlife, and visual quality (table 1). These ratings are only relative, and they were determined by different factors for each resource. Productivity, present and future stand conditions, and expected future importance were considered. For example, jack pine on site index 70 is rated low for timber because these stands are usually converted to more productive red pine at the end of the rotation; this is reflected further in the high ratings for red pine. Depending on the viewpoint of the landowner or manager, however, the ratings could be quite different. The wildlife ratings include both "edge"

Table 1.—*Importance of the aspen, birch, and associated conifer forest types for providing timber, water, wildlife, and visual quality on a per-unit basis*[1]

Forest type and site index	Area (million acres)	Resource				
		Timber	Water	Wildlife		Visual quality
				Edge species	Interior species	
Aspen	13.2					
Site 80		H	H	H	L	M
Site 65		M	H	H	L	M
Site 50		L	H	H	L	M
White birch	1.8					
Site 70		M	H	H	L	H
Site 60		L	H	H	L	H
Site 50		L	H	H	L	H
Red pine	1.2					
Site 75		H	M	L	H	H
Site 60		H	M	L	H	H
Site 45		H	M	L	H	M
White pine	0.5					
Site 75		H	M	M	H	H
Site 60		H	M	M	H	H
Site 55		M	M	M	H	M
Jack pine	2.5					
Site 70		L	M	M	M	L
Site 55		H	M	M	M	L
Site 40		M	M	M	M	M
Spruce-fir	2.9					
Site 60		H	L	M	M	M
Site 40		M	L	M	M	M
Site 20		L	L	M	M	L
Black spruce	2.1					
Site 45		H	L	M	L	L
Site 35		H	L	L	M	M
Site 25		M	L	L	M	H
Northern white-cedar	1.9					
Site 40		M	L	M	H	M
Site 30		M	L	M	H	M
Site 20		L	L	L	M	L

[1] H = high; M = medium; L = low.

species (those associated with forest edges, openings, shrubs, and ground vegetation), and "interior" species (those associated with maturing and old-growth forest stands) (see Appendix 2).

Second, for each of the forest types, we rated some common harvest options according to their effect on timber investment return, water, wildlife, and visual quality (tables 2-9). The ratings in each table permit the owner or manager to compare— *within the forest type*— the general effects of each harvest option on the various resources. A harvest option was rated "excellent" if its effect on a resource was most desirable for that resource. Conversely, a practice was rated "unfavorable" if it would diminish the resource.

Third, we summarized pertinent information and the consequences of harvest options for each forest type.

When complete information on the consequences of a harvest option was not available, we described the most likely impact of the harvest option on the resource in question.

We used only common names of plants and animals (except for a few diseases) throughout the report; however, scientific names are listed in Appendix Table 1.

ASPEN

Type Description

Aspen is the largest and most widely distributed of the forest types, covering about 13 million acres. The dominant species is quaking aspen, a small to medium-sized tree; it can grow in essentially pure stands, but other species are usually present in varying numbers. Common associates are bigtooth aspen, white birch, northern red oak, red maple, balsam poplar, jack pine, balsam fir, spruce, and northern white-cedar.

Aspen occupies diverse soils and sites, and its growth rate varies with soil fertility and available moisture. Tree heights at age 50 range from 90 feet on deep, fertile, high-calcium loams to 40 feet on dry sands and rock outcrops or water-logged mineral soils and peats (Brinkman and Roe 1975).

Aspen is aptly described as the "phoenix tree"; it has persisted in natural stands largely because of fire. Even where it is a minor component of the stand, aspen's ability to produce abundant root suckers often enables it to become the dominant species after logging or fire. Where aspen is already dominant, it easily reestablishes itself after logging, especially when cutting is followed by fire or similar treatments to kill back other vegetation.

Because aspen cannot reproduce successfully under its own shade, it is replaced by other species when natural ecological succession is not interrupted by fires, logging, or windstorms. On relatively dry sites, aspen is succeeded by red maple or oaks. On moist, fertile soils, aspen is followed by balsam fir, white spruce, or white pine, and on the wetter sites by balsam fir, black spruce, or northern white-cedar. Succession will be to northern hardwoods where that type occurs.

Aspens produce good seed crops every 1 to 5 years, and seedlings can become established only when cutting or burning prepares a suitable seedbed and continuous moisture is provided. However, regeneration is nearly always assured by the abundant root suckers that develop after trees of any age are cut or killed. Vigorous suckers grow fast enough to overtop competing vegetation of comparable age, but they cannot persist under the shade of shrubs or taller reproduction. Although aspen stands continually produce small numbers of suckers, these seldom survive long under a canopy.

Aspen stands typically contain well-developed shrub and herb layers. Plant species diversity is usually greater in this type than in any of the associated conifer forest types.

Evaluation and Discussion (see table 2)

Timber

Because aspen grows on sites ranging widely in productivity, resource objectives should be tailored accordingly. Site index 50 stands are not capable of producing economic quantities of pulpwood to the traditional industry standard of a 4-inch top; but these stands, when fully stocked and managed for whole-tree utilization in 35-year rotations, can produce an equivalent fiber volume of 50 ft 3 /acre/year as chips. For most aspen sites pulpwood should be the main product objective, and the highest investment returns are realized from rotations of about 35 years. On the other hand, a few good aspen sites (exceeding site index 80) mostly in the northern Minnesota counties can be managed for sawtimber and veneer bolts on rotations of 50 to 60 years. Since aspen commonly suffers high losses to heartrot after age 50, intermediate thinnings can be used to shorten rotations and greatly increase yields of large logs (Perala 1977). Good sites may also be managed on a short-rotation basis (30 years) with whole-tree logging and chipping.

Clearcutting to regenerate the stand by suckering is the best means of perpetuating the type. Limiting clearcut size to accommodate other forest uses tends to increase costs, especially in clearcuts smaller than 5 to 10 acres. Aspen growth in extremely small clearcuts (2 acres or less) is strongly retarded by adjacent, older stands.

Table 2.—*Effects of some aspen harvest options on forest resources—a desirability rating*[1] *(timber management objectives: pulpwood, sawtimber, and veneer)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Even-aged management with clearcutting; no intermediate thinning; Pulpwood objective	35	1	U	0	0	++	U	+
		5	U	++	0	+++	U	+
		20	++	+++	0	++	U	+
		50	+++	+++	0	++	U	+
	45	1	U	0	0	++	U	+
		5	U	+	0	+++	+	+
		20	+	++	0	+	++	+
		50	++	++	0	+	++	+
Even-aged management with clearcutting; no intermediate thinning; sawtimber objective (6" top)	50	1	U	0	0	++	U	++
		5	U	+	0	+++	+	++
		20	++	++	0	+	++	+
		50	+++	++	0	+	++	+
	60	1	U	0	0	+	U	+++
		5	U	+	0	++	++	++
		20	+	++	0	+	+++	+
		50	++	++	0	+	+++	+
Even-aged management with clearcutting; intermediate thinning; Veneer and sawtimber objective (8" top)	50	1	U	0	0	++	U	+++
		5	U	+	0	+++	U	+++
		20	++	++	0	+	++	++
		50	+++	++	0	+	++	+
	60	1	U	0	0	++	U	+++
		5	U	+	0	+++	+	+++
		20	+	++	0	+	++	++
		50	++	++	0	+	++	+
No harvest			0	0	0	U	+	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

Because site index 50 stands are only marginally useful for aspen production, these and poorer sites are more suited to conifers and should be converted where timber production is the prime objective.

Water

Aspen and other hardwood types contribute more water to streamflow or ground water recharge than any other forest cover. Clearcutting this type increases water yield, and harvesting blocks of 20 to 50 acres at shorter intervals will increase water yield more.

As long as water influence-zone restrictions (or equivalent precautions on non-Federal land) are adhered to, and logging roads are constructed with care, no serious erosion hazard results from clearcut logging in aspen, nor do nutrient concentrations in streamflow change significantly (Verry 1972, Richardson and Lund 1975).

Wildlife

The importance of the aspen forest type for game species such as the white-tailed deer, ruffed grouse, and woodcock has long been recognized. However, the type also provides important habitat for a variety of other edge wildlife species. In contrast to "edge species" it generally provides poor habitat for interior species.

Maintaining intolerant types like aspen is important in managing for wide-ranging edge species such as white-tailed deer and moose. For good game habitat, McCaffery (1970) recommended 5 percent upland brush or grass, 10 percent scrub oak, 25 percent aspen, 15 percent conifer cover, and 5 percent lowland brush, or 40 percent combined acreage of grass, upland brush, scrub oak, aspen, and jack pine. However, the area should not have more than 30 percent northern hardwoods or 30 percent pine plantation, or 45 percent combined acreage of northern hardwoods, pine plantation, and white birch. Byelich *et al.* (1972) recommended slightly higher proportions of intolerant types for deer in Michigan: a minimum of 15 percent forest openings and 35 percent aspen, or 60 percent openings, upland brush, aspen, oak, and jack pine combined. For moose, Peek *et al.* (1976) recommended township-sized blocks vegetated with 40 to 50 percent aspen-birch under 20 years old, 35 to 50 percent aspen-birch over 20 years old, and 5 to 15 percent spruce-fir. For species with small home ranges and particularly for those living totally within an aspen stand, the mix of types is not as important, except where broad-scale forest type conversion is contemplated. The foregoing type mixes are idealized objectives, and an owner's soil type or current stand composition may dictate a somewhat different composition.

Because plant composition changes as the stand matures, it may provide for the requirements of a wildlife species during some periods and at others actually be detrimental. This means that the number and distribution of stands of various ages is also important. For example, all age classes are important to ruffed grouse; therefore it is important not only to have aspen stands, but to have them in different age classes (stands up to 10 years old serve as brood habitat, stands 10 to 25 years old serve as over-wintering and breeding habitat, and stands over 25 years old provide nesting cover and winter food). Gullion and Svoboda (1972) recommended that for ruffed grouse, aspen should be clearcut on a 40- to 50-year rotation in a manner such that about 10 acres in a 40-acre unit is cut every 10 years. In so doing, male aspen clones should be preserved for winter food. For other wildlife, only certain age classes may be important. For example, Byelich *et al.* (1972) suggested that 25 percent of the aspen type be maintained in the 0- to 10-year age class as food for deer, especially where it is adjacent to lowland conifers used by deer for winter cover. In fact, since the value of aspen to deer declines with stand age, circumstances may warrant short-rotation management of aspen near wintering areas— i.e., a 25- to 30-year rotation with a cutting interval of 5 to 10 years.

The size of cutting unit is also important. For deer, a harvest unit should preferably be smaller than 40 acres (Ruske 1969). In fact, McCaffery and Creed (1969) found more intense deer use in permanent openings 0.5 to 5 acres in size than in larger openings, and in openings less than 300 feet wide. Similarly, Wetzel *et al.* (1975) found light use in areas farther than 130 feet from cover. This suggests that small patches and strips of different age classes are more beneficial to deer than large openings (Telfer 1974). Peek *et al.* (1976) recommended units of at least 200 acres for moose. Thus, not only do moose tolerate larger cutting units, but they require larger units than deer.

Aspen is also preferred by beaver; stands should be situated within 300 feet of shoreline areas, and preferably within 100 to 200 feet. Knudsen (1962) estimated that about 5 acres of timber should be available at the average colony. At an average distance of 150 feet, this means that 1,500 feet of shoreline aspen would be required to sustain an average colony. Young aspen stands are not only preferred by beaver, but are utilized more thoroughly.

Aspen stands of all age classes are suitable for a large variety of smaller "edge" vertebrates. While the needs of some may be restricted to certain age classes, the needs of most can generally be met with a balanced distribution of age classes in time and space. For cavity nesters, standing dead snags can be left at harvest; these also serve as feeding and perching sites for other birds. For interior species, longer rotations or no cutting at all may be desirable.

Visual Quality

The aspen leaf has an unusual petiole attaching it to the stem, providing its common name "quaking aspen". The rippling of aspen leaves, even in very light wind, has an appealing aesthetic quality, and in spring the pastel foliage provides a pleasing contrast to the darker surroundings. Aspen's autumn foliage is also very attractive; varying blends of golden leaves and whitish bark contrast with the dark green of associated conifers or the bright colors of other hardwood species (Brinkman and Roe 1975).

Because the aspen type is so extensive and because it is usually maintained through clearcutting, management practices have an important effect on visual quality, especially in scenic areas, travel corridors, recreational use areas, and along water bodies. In addition to close control of logging operations, other important factors to be considered in aspen harvest include viewing distance, size, shape and distribution of clearcuts, timing of operations, and establishment of vistas.

The foreground (about 0 to mile) and the middleground (about to 5 miles) viewing zones are most important because they are most readily seen. The background zone about 3-plus miles is important when it is highly visible and when it provides a scenic backdrop.

Foreground landscapes can be enhanced by:

1. Providing vistas that expose and frame scenic features.
2. Utilizing clearcuts to create visual variety by opening up dense stands and breaking up straight lines of timber with curved lines and irregular openings.
3. Leaving attractive and special-interest trees and snags.
4. Providing variety in plant species, age class, tree size, and type.
5. Softening edge layout with transition vegetation.
6. Varying the sizes and shapes of cuttings.
7. Converting to other vegetative types.
8. Treating logging slash.

An aspen regeneration cut presents less visual impact if its size does not dominate and if it is blended with natural or man-made openings that occur in the landscape. The apparent size of cutting units can be reduced by restricting the amount of cut area seen from any one viewing position. Factors such as distance, shape, and screening provided by intervening ridges or other landforms and islands or clumps of vegetation help to limit the apparent size of cutting units.

Irregular, free-form shapes that follow natural projections, indentations, soil boundaries, and topographic features expose smaller areas of clearcut to view. Long, straight, unnatural edges or geometric shapes that clash with natural landscape forms should be avoided.

The outline of an opening that has sharp edge contrast between the clearcut area and surrounding timber can be "feathered" to soften the impact. Existing openings can be used as part of edge, and adjacent stands can be thinned to develop an irregular appearance and spacing. Retaining plant species of various sizes and textures will help to soften edge.

Uniformly spaced clearcuts of nearly the same size and shape are seldom visually pleasing. Dispersal and irregular spacing should be used to avoid a repetitious pattern.

Aspen harvests should be scheduled so that enough time elapses before adjacent new areas are cut to allow dulling and greening of the disturbed areas. Stands immediately adjacent to previous clearcuts should not be scheduled for a regeneration cut until a stand of trees has been established. This manipulation of age classes will create variety and contrast in the sequence of cutover areas.

Where worthwhile opportunities exist, consider cutting carefully selected trees or groups of trees or utilizing clearcuts to open vistas through the timber. This can provide temporary or permanent views of outstanding physical features (rock outcrops, lakes, streams) and panoramas of the forest landscape. Leave clumps of birch and spruce or other conifers to frame and give scale and dimension to the view. Vista openings need not be permanent. As changes occur in the forest scene, new openings can be developed to show the best views. Less attractive views can be allowed to close in.

Harvest options that involve long rotations with intermediate thinnings will have less impact on visual quality than those requiring short rotations. The no-harvest option will result in eventual conversion of the type through natural succession to more tolerant species. As part of this process, the aspen stand frequently breaks up rapidly, revealing dead trees and broken stems that may be unattractive to many viewers.

Diseases

Aspen managed on a 35-year rotation will host a number of diseases that kill very young trees. However, in dense sucker stands none of these diseases will affect future stocking of the mature stand, because they will act as thinning agents.

Shepherd's crook shoot blight sometimes causes terminal shoot dieback during the stand's first few years and often appears capable of wiping out a young stand. However, this disease seldom causes significant mortality. Instead, it reduces growth by killing the current year's terminal shoot, causing a bush-like appearance. Aspen suckers become much less susceptible to shoot blight after they are 5 to 10 years old, and then resume normal height growth.

Hypoxylon canker is one of the principal causes of aspen mortality during a pulpwood rotation. This disease kills an average of 1-2 percent of the aspen trees in a stand yearly, but if a dense sucker stand is obtained after a clearcut, the disease will act primarily as a thinning agent. Susceptibility of aspen to *Hypoxylon* canker varies by genotype. Highly susceptible clones (with 25 percent or more of the stems infected) should not be regenerated to aspen unless a significantly more resistant clone can be encouraged to invade the area occupied by the susceptible clone. One way to avoid regenerating these clones is to leave them uncut. A leaflet on how to identify *Hypoxylon* canker (Schipper and Anderson 1976) is available from the North Central Station on request.

Aspen managed on 50- to 60-year rotations will be subject to the same diseases that affect aspen on shorter rotations. In addition, white trunk rot will begin to be a problem between age 40 and 50, and stands should be checked occasionally to determine whether they must be harvested early to avoid breakup. Trunk rot will have a much greater impact during the last 10 years of a 60-year rotation and may begin to cause significant stand breakup unless the stands are checked regularly and regenerated before rot damage becomes excessive.

Wetwood (caused by bacteria) will become prevalent in older trees. While this disease does not kill trees, it will result in collapse of lumber during kiln drying.

Perennial cankers will render portions of affected trees unsuitable for veneer even though they do not kill trees. Intermediate thinnings to produce veneer-quality trees may cause increased incidence of both *Hypoxylon* canker and white trunk rot. Careless thinning that wounds remaining aspen will increase other heart rots. Therefore, once thinning begins, stands should be checked periodically so that they can be harvested early if either of these diseases begins to cause significant amounts of dead wood.

Although viruses of aspen have not been studied extensively, there is some evidence that they may account for clone deterioration in some areas when aspen is repeatedly regenerated from root suckers (Berbee and Castello 1976).

Insects

Although more than 300 species of insects feed on aspen (Davidson and Prentice 1968, Batzer 1972), only a few are important. Juvenile aspen can be heavily attacked by stem borers, but if regeneration is dense, sufficient stems usually escape damage to provide a well-stocked stand. If suckers are excessively dense these attacks may provide a natural thinning.

The most spectacular insect defoliator of aspen is the forest tent caterpillar. Widespread infestations of this insect defoliate aspen stands at 6- to 16-year intervals, but cause noticeable mortality only on excessively wet or excessively dry sites. Infestations do cause reduced growth, accelerated nutrient cycling, and temporary release of understory herbs, shrubs, and tree reproduction, however. The forest tent caterpillar is likely to cause significant economic impact only when aspen is grown for sawtimber and veneer.

The large aspen tortrix is another defoliator that has violent but short-lived population upsurges. Little tree growth is lost, however, because heavy infestations seldom last more than 1 or 2 years.

The poplar borer causes damage primarily in open-grown stands. Trees can break when weakened by tunneling of the large larvae. Sawtimber and veneer management options would be affected most. Treatment for the borer with insecticide is not feasible.

WHITE (PAPER) BIRCH

Type Description

The white birch type is estimated to occupy about 1 million acres in the Lake States (Quigley and Babcock 1969). White birch seldom develops into a large or high-quality sawtimber tree, and most of it is harvested as boltwood and used for sawed specialty products or pulpwood (Quigley and Babcock 1969).

White birch is an intolerant tree, more so than its common associates white spruce and balsam fir, but it may persist in successionally advanced stands through its ability to fill the canopy gaps created by death of surrounding trees.

White birch is a short-lived, fast-growing tree. Trees of seedling origin reach maturity as early as 60 years of age, and maximum age is about 140 years. Sprouts are shorter-lived and usually mature at 50 to 60 years, with a maximum age of 70 to 90 years. In mature stands, the trees attain an average height of 70 to 80 feet and an average diameter of 10 to 12 inches.

While white birch occupies all elevations, slopes, and aspects in this region (Fowells 1965), site quality— at least in northern Wisconsin— is closely related to topography (probably as a reflection of soil moisture conditions). Poorer sites occur on steeper slopes and on ridgetops, while better sites occur on flats and rolling terrain. Site quality also increases with increased soil silt and clay and with mottling in the upper 48 inches of soil (Cooley 1962).

White birch resembles aspen in many respects and frequently grows along with aspen in similar secondary successions (Curtis 1959). Its importance as wildlife habitat and as an aesthetic resource may exceed its value for wood fiber.

Like the aspen type, white birch stands typically support a well-developed tall shrub and herbaceous layer; many species are common to both types.

Evaluation and Discussion (see table 3)

Timber

Where white birch is grown for pulpwood, maximum annual yields are realized on rotations of 45 years on the best sites, and 70 years on the poorest commercial sites. Financial maturity is generally reached 5 to 10 years earlier. However, when white birch is grown in mixture with other pulpwood species (the usual case), it is best to apply the same rotation used for the other species and harvest the entire forest crop at the same time. Only site indexes of 60 and better should be considered for growing white birch for sawtimber or boltwood. Early tending of stands (weedings, cleanings) and intermediate thinnings (if very carefully done) will improve quality, increase yields, and shorten rotations by about 10 to 20 years, depending on site and desired product size.

Using scarification along with a shelterwood system or a progressive 1-chain-wide strip clearcutting is probably the best way to regenerate the birch type from seed in the Lake States. Trees less than 60 years old reproduce well by stump sprouting. Where uneven-aged management is used white birch will be steadily replaced by more tolerant species.

Water

Comments for the aspen type (page 9) apply equally well to the white birch type; both aspen and white birch are deciduous hardwoods with relatively short rotation ages, and they frequently occur together.

Wildlife

The relatively high value of white birch to edge wildlife species is probably related to the variety of tall shrub and herbs in this type. Although white birch itself is less preferable than aspen, the components of the white birch type are otherwise very similar to those of the aspen type. Likewise, the wildlife community is similar in both, except, for example, the additional attraction white birch offers to the yellow-bellied sapsucker. A leaflet on how to identify sapsucker injury to trees (Ostry and Nicholls 1976a) is available on request. As with aspen, white birch also provides poor habitat for interior species of wildlife.

Recommendations for wildlife discussed under aspen management (pages 9-10) generally apply to the white birch type as well. However, in certain areas, the higher monetary value of white birch may permit the cautious use of intermediate thinnings. For many edge wildlife species, this practice would be beneficial because release cutting stimulates ground vegetation and seed production on the remaining trees for about 10 years (Shaw 1969). For example, Shaw and Ripley (1965) found that the number of woody twigs on browse plants doubled when the basal area of the overstory was reduced from 110 to 80 square feet per acre. Thus, for wildlife purposes Shaw (1969) recommended making intermediate cuts in white birch stands at 10-year intervals and keeping 25 percent of the stand in the seedling-sapling age class.

Visual quality

White birch is one of the most striking native North American trees. The bark of young trees is reddish brown and not particularly attractive, but it becomes white as the tree matures and tends to peel about the trunk in curled strips. Foliage colors are pleasing to the eye in spring and summer, but especially in fall when the leaves turn a vivid yellow. Clumps of trees are often formed from stump sprouts, making white birch easy to see and adding contrast and variety to the landscape (Noyes 1969).

Table 3.—*Effects of some white birch harvest options on forest resources—a desirability rating*[1] *(timber management objectives: pulpwood, sawtimber, and veneer)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Even-aged management with clear-cutting; no intermediate thinning	50	1	U	0	0	+	U	++
		5	U	+	0	++	U	++
		20	U	++	0	+	++	++
		50	+	++	0	+	++	+
	70	1	U	0	0	+	U	++
		5	U	+	0	++	+	++
		20	++	++	0	+	++	+
		50	+++	++	0	+	++	+
	90	1	U	0	0	+	U	+++
		5	U	+	0	++	++	++
		20	+	++	0	+	+++	+
		50	++	++	0	+	+++	+
Even-aged management with clear-cutting; intermediate thinning	30	1	U	0	0	++	U	++
		5	U	++	0	+++	U	++
		20	U	+++	0	++	U	++
		50	+	+++	0	++	U	+
	50	1	U	0	0	++	U	+++
		5	U	+	0	+++	U	+++
		20	++	++	0	++	+	++
		50	+++	++	0	++	+	+
	70	1	U	0	0	++	U	+++
		5	U	+	0	+++	U	+++
		20	+	++	0	+	+	++
		50	++	++	0	+	+	+
No harvest			0	0	0	U	+	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

White birch is attractive as a single stem, in clumps, in pure stands, or in mixed stands. Associated species, such as balsam fir, spruce, or white pine, also add to its visual appeal. These associates, when not dominating the stand, add a visually pleasing dark green contrast to the birch (Noyes 1969).

Cultural practices can enhance the visual quality of white birch stands. Even-aged management with clearcutting and careful thinning is recommended, but large clearcuts should be avoided. The harvest practices suggested for aspen, pages 10-11 apply to the white birch type as well. Managers should especially take advantage of the ability of birch to develop clumps of stems from stump sprouts (Noyes 1969).

The no-harvest option would result in conversion of the white birch type to more tolerant species through natural succession. Thus, under this option stands would provide maximum visual quality for a relatively short period— from maturity to onset of stand break-up.

Diseases

Phellinus trunk rot is the principal agent responsible for white birch cull. This heart rot is most important in the older stands.

Poria causes a canker and heart rot in older white birch stands. Affected portions of *Poria*-cankered stems will be unsuitable for veneer.

Birch dieback may be important for all birch harvest options because it can kill entire birch stands. The cause of birch dieback is unknown. Intermediate thinnings, if too severe, can cause reduced growth of the remaining trees and breakup of the stand.

Insects

Many insects feed on white birch, but the one capable of the most widespread infestations in the Lake States is the birch skeletonizer. Because defoliation occurs late in the growing season, little mortality results.

An eastern pest, the birch leaf miner, is moving west and may now be found hollowing out leaves in Lake States birch stands. Weakened trees become susceptible to infestations of the bronze birch borer, which can kill them (Baker 1972). Long rotations would expose stands to recurrent outbreaks of all three insects.

RED PINE

Type Description

Red pine was an important component of the extensive Lake States pine forests that were cut about the turn of the century. Logging was generally followed by slash fires, either accidental or intentional, to reduce the risk of wildfires. The widespread fires increased aspen and jack pine at the expense of red pine and white pine. Although the area of natural red pine forest today is small, the type has been expanded considerably by planting; it now occupies a total area of about 1 million acres.

Red pine is most common on level to gently rolling topography underlain by fine to loamy sands, or on low ridges adjacent to lakes and swamps. It grows best on moist, well-drained soils, but can withstand moderate drought. Nearly all red pine stands in Minnesota are found on site indexes between 45 and 75. Average site index is 55 at 50 years of age.

Red pine grows in both pure and mixed stands. Associated species on the coarser, drier soils are jack pine, aspen, white birch, and northern pin oak. On the fine to loamy sands, associates include eastern white pine, red maple, northern red oak, and white spruce-balsam fir mixtures.

Because of its longer lifespan, red pine often succeeds its less tolerant associates. In the absence of a major disturbance, it is succeeded by its more tolerant associates because they can regenerate in the understory more easily. The rate of succession is more rapid on the better sites.

Under natural conditions, wildfires commonly interrupt ecological succession in red pine. Pure red pine stands sometimes regenerate following fire, but a mixture of intolerant species often results. Fire easily kills young trees, but older ones usually survive ground fires because of their thick bark. Fire scars on old-growth trees attest to the common historical occurrence of fire in this type.

Red pine stands seldom survive more than 200 to 250 years, but a few live to 350 and some to about 400 years.

Common shrubs include hazel, blueberry, sweet-fern, willow, cherry and bush-honeysuckle. Common herbaceous species include aster, bracken fern, wintergreen and false lily-of-the-valley.

Evaluation and Discussion (see table 4)

Timber

Red pine is unique in the Lake States in that it is the only type managed to a major extent as an intensively cultured plantation crop. This is due to its relatively fast growth rate and productivity, markets for thinnings and its high economic value over a wide range of sites. Common product objectives are pulpwood, posts, poles, and pilings from intermediate thinnings, and sawtimber from the final crop, even on site indexes as low as 45 (which, for example, would be noncommercial for aspen).

Although it is possible to grow red pine using an uneven-aged system, even-aged management provides optimum timber production because the species grows best in full sunlight. Basal area densities of 90 to 180 ft²/acre, depending on site and tree size desired, should be maintained by intermediate thinnings. A basal area of not more than 90 ft² /acre appears optimum for obtaining the highest investment return (Lundgren 1965). Where markets support thinnings, rotations for highest investment returns can vary from 65 to 95 years. The decline in financial return is gradual from 95 to 125 years.

Investment returns from growing red pine in the Lake States are thoroughly detailed in North Central Forest Experiment Station Research Papers LS-18 and NC-2 (Lundgren 1965, Lundgren 1966).

Clearcutting followed by planting is recommended unless continuous tree cover is needed. In esthetically sensitive areas, strip-shelterwood systems with planting allow a gradual transition from mature stands to new forest.

Water

Evaporation and transpiration losses are higher in pure pine stands than in hardwood stands. Thus, pine stands yield less streamflow than hardwood stands. A quick estimate of differences in streamflow between hardwoood and pine stands can be calculated using North Central's Research Paper NC-128 (Verry 1976). Thinning dense pine stands can increase water yield if water production is a primary goal (Urie 1971, Van Der Zel 1970).

Many young plantations require herbicide applications to control competing broadleaf species. There are, however, no serious water quality hazards associated with forest applications of herbicide, unless there are accidental spills of concentrated herbicide in a stream. Direct delivery of herbicide to surface waters should also be avoided.

Wildlife

The lack of variety in species and stand structure and the long life of the red pine type creates conditions generally unfavorable to edge wildlife, but favorable to interior wildlife. Red pine provides the best habitat for edge wildlife during the early stages of regeneration. However, this period is brief, especially in extensive plantations. During the rest of the life of homogeneous stands, the

Table 4.—*Effects of some red pine harvest options on forest resources—a desirability rating*[1] *(timber management objectives: pulpwood, poles, and piling from periodic thinnings; sawtimber final crop)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Even-aged management with intermediate thinnings and clearcutting	75	1	U	0	0	++	U	++
		5	+	+	0	+++	U	++
		20	++	++	0	+	+	+
		50	+++	++	0	+	+	+
	110	1	U	0	0	++	U	+++
		5	+	+	0	+++	+	+++
		20	+	++	0	U	++	++
		50	++	++	0	U	++	++
	145	1	U	0	0	+	U	+++
		5	U	+	0	++	++	+++
		20	+	++	0	U	+++	++
		50	++	++	0	U	+++	++
No harvest			0	0	0	U	++	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

value to edge wildlife remains low. In contrast, the primary value to interior species occurs during the period of stand maturity.

Certain management practices can be applied to enhance the value of the red pine type for edge wildlife. Because red pine can provide cover for a number of species, plantations can be established in areas short of coniferous cover. However, to be beneficial to edge wildlife, red pine should not occupy more than 30 percent of the area (McCaffery 1970).

Plantation size is also important. Bailey and Alexander (1960) recommended that conifer plantations not exceed 7 acres. They should preferably be as small as 1 to 5 acres if well interspersed with hardwood types (Smith 1958). If these small sizes are not suitable to overall objectives, Rutske (1969) recommended that plantations be surrounded by 60-foot-wide unplanted strips, and in plantations nearing 10 acres or larger, he suggested alternating 60-foot-wide unplanted strips with 250- to 400-foot-wide planted strips. Other practices that can benefit edge wildlife include (1) 10-foot rather than 6-foot spacing where Christmas trees are not an objective, (2) several rows of spruce around the perimeter to reduce interior wind velocities, (3) mixing the species composition by alternating 20 rows of red pine with 10 more widely spaced rows of other conifers, and (4) maintaining small openings and hardwood inclusions (Smith 1958). The main objective of these measures is to avoid extensive, dense stands with little or no ground vegetation. As the stand matures, intermediate cuttings to minimum recommended stocking levels can help to maintain a ground vegetation layer beneficial to edge wildlife.

With one exception, none of the preceding measures recommended for edge species should affect the suitability of red pine for interior species. This exception is the creation of small, isolated patches of red pine that may not be as favorable as larger stands in closer proximity to one another. The other measures would tend to be beneficial by increasing vegetation diversity, crown vigor of the overstory, and seed production. Bald eagles and ospreys require live and dead old-growth red and white pine near water, and it is prudent to reserve from cutting an area of about 7 acres surrounding existing and potential nest sites.

Visual Quality

Red pine trees, especially large ones along lakes or streams, are very attractive. Red pine stands are most pleasing when managed near the upper limits of basal area, which reduces the amount of understory vegetation.

To maintain visual quality, careful silvicultural operations and implementation of those items discussed under the aspen type (pages 10-11) should be encouraged. Maximum visual quality will be maintained by selecting management options that provide high stand basal areas over long rotations. If visual quality is a major consideration, understory vegetation can be controlled to enhance the park-like appearance, especially in younger or thinned stands, including plantations.

The no-harvest option will maximize visual appeal for any single area because of the longevity of the species, although without thinning it will take longer to reach large diameters. In the long run, however, the type will normally undergo conversion to more tolerant species through natural succession.

Diseases

The most important disease of red pine in the Lake States at present is *Scleroderris* canker. A leaflet explaining how to identify this disease is available from the North Central Station on request (Skilling and O'Brien 1973). The disease is most important in young plantations, where it causes shoot dieback and canker, and can kill all the trees in a plantation. Once the trees have become taller than about 6 feet, they generally are not affected by *Scleroderris* canker in the Lake States. Recently a new form of *Scleroderris* canker has been encountered in New York state that is killing much older trees.

Red pine shoot blight is an important disease of red pine reproduction when seed trees or shelterwood trees are left. The disease kills the current year's needles, and if severe, will kill the entire tree. A leaflet telling how to identify this disease is available from the North Central Station on request (Skilling and O'Brien 1973).

Lophodermium needlecast disease can infect red pine of all ages, but is most important in seedlings and saplings. The disease can kill young trees if severe and will stunt the growth of less severely infected trees. *Scleroderris* canker, shoot blight, and needlecast are the only diseases that reduce visual quality of affected stands under any of the management options.

Red pine root and butt rot *(Armillaria)* can infect red pine when the trees have been under stress from environmental or pathological conditions. The disease is most severe when red pine plantations are established in areas where hardwoods were grown previously, but can be important in areas occupied by conifers for many years.

Polyporus schweinitzii also causes a root and butt rot; it enters through wounds caused by fire or logging. Therefore it can be important in stands that are periodically thinned.

Fomes root rot can infect red pine of all ages, but it is not important in this region at present.

Fomes red pine heart rot infection usually enters through dead branch stubs, while wounds rarely become infected.

Recently *Diplodia* has become an important disease of red pine. This fungus kills new shoots and branches, and in some situations girdling cankers will kill trees.

Insects

Insect damage to red pine is most prevalent during the establishment period. In plantations, white grubs, the red-headed pine sawfly, and the Saratoga spittlebug are probably the most serious. Also, in the eastern and southern parts of the red pine range, the European pine shoot moth can cause damage to leaders, although wood fiber growth loss may be recovered in succeeding years (Miller *et al.* 1978). No serious problems from insects occur once the trees reach pole size. However, cone crops are frequently destroyed by insects (Mattson 1971). A leaflet on how to control the red pine cone beetle is available on request (Miller and Taylor 1968).

WHITE PINE

Type Description

Eastern white pine, the mainstay of the early logging era in the Lake States, is now of minor importance as a timber species. Throughout most of the region today, it is threatened by white pine blister rust. Thus, white pine is infrequently planted, and planting will not likely increase until rust-resistant stock becomes readily available. White pine occurs in scattered natural stands throughout the region, or more frequently as a component of other types—either as a super-canopy or scattered individuals, or as a dominant or codominant component of red pine stands.

White pine grows on a wide variety of sites. Optimum development is on moist, deep loams or on sandy loams of lower slopes, but it also is able to compete on upper slopes and ridgetops.

Within densely stocked pure or nearly pure stands of white pine, the tall shrub layer is poorly developed, except for hazel; a low shrub layer of bush-honeysuckle, sweet-fern, and blueberry predominates over a sparse herbaceous ground cover.

Evaluation and Discussion (see table 5)

Timber

Although no longer the giant in the timber industry that it once was, white pine still commands economic respect where significant amounts of it are available in large stands. It is prized for its high-quality lumber and rapid growth rate, sometimes even in the face of high risk from biological hazards such as blister rust (Schlaegel 1971). White pine is not well suited for pulpwood or poles, and sawtimber is the major product objective (other than Christmas trees).

Although uneven-aged management is possible for white pine, it has not proven very satisfactory for regeneration; thus we recommend even-aged management. Clearcutting during good seed years or in small patches or strips when seed is available from adjacent stands is moderately successful. If no regeneration develops, mechanical site preparation and planting are required. Spreading shelterwood cuttings over a period of years is probably the most reliable method for natural regeneration.

Rotations vary but 80 years is sufficient to produce large saw logs.

Water

Comments under red pine (page 15) apply equally well to white pine. In addition, some good

Table 5.—*Effects of some white pine harvest options on forest resources—a desirability rating*[1] *(timber management objectives: sawtimber)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Even-aged management with clear-cutting	80	1	U	0	0	++	U	++
		5	+	+	0	+++	+	++
		20	++	++	0	+	++	+
		50	+++	++	0	+	++	+
	120	1	U	0	0	+	U	+++
		5	+	+	0	++	+	+++
		20	+	++	0	+	+++	++
		50	++	++	0	+	+++	+
No harvest			0	0	0	0	++	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

white pine stands occur on lower slopes in moist stream bottoms. Water influence zone restrictions on Federal land should be adhered to (with equivalent precautions elsewhere), and erosion from roads should be avoided by placing roads away from seepage areas or by providing adequate drainage.

Wildlife

In comparison with the red pine type, the white pine type (if not in pure, dense stands) tends to have better-developed tall shrub and herb layers. This consideration and the more mesic soil conditions tend to give the white pine type higher value than red pine for edge wildlife species, while still maintaining considerable value for interior wildlife. As with red pine, the white pine type also provides the best habitat for edge wildlife during the early stages of regeneration.

Management recommendations for wildlife follow those previously described for red pine (pages 15-16). However, in view of the small amount of reforestation with white pine, management opportunities consist primarily of maintaining tall shrub and herb layers by thinning, and preserving 7 acres around existing and potential nest sites for bald eagles and ospreys.

Visual Quality

Mature white pine, with its plume-like branches, is visually attractive along waterways, in small groves, or as single trees. Because white pine is generally found on mesic sites, it does not often exhibit the open, park-like understory of old-growth red pine stands.

Management options that call for harvest of smaller areas and longer rotations will maintain the greatest visual quality, and special care must be taken in newly regenerated stands.

Dead portions of white pine crowns infected with blister rust are not necessarily unattractive for all viewers, but the life of individual trees can be prolonged by pruning infected or dead branches (Hansen *et al.* 1974).

The no-harvest option will provide high visual quality for a long period in the absence of blister rust. Eventually, however, the type will be lost under this option because of natural succession to more tolerant species.

Diseases

White pine blister rust is by far the most important disease of eastern white pine, limiting its management to areas of low blister rust hazard (VanArsdel 1964), at least until resistant varieties are developed.

Fomes pine heart rot is responsible for about 90 percent of the cull in eastern white pine. The disease enters through dead branch stubs and weevil-killed shoots.

Armillaria pine root and butt rot will be important only in white pine plantations established in areas where hardwood stumps are left from the previous harvest.

Under the no-harvest option, white pine blister rust and *Armillaria* pine root rot will be important from a visual standpoint because they kill trees.

Insects

The two most significant insects in white pine management are the white pine weevil and the introduced pine sawfly. The weevil damages leaders, resulting in deformed stems. The incidence of weevil attack is reduced where there is an overstory of broadleaf trees. The sawfly defoliates trees of all ages and can reduce growth and kill the tops of mature trees.

JACK PINE

Type Description

The jack pine type covers about 2.5 million acres in the Lake States. Jack pine grows in both pure and mixed stands; common associates in mixed stands are red and eastern white pine, the aspens, white birch, several oaks (mainly northern red oak and northern pin oak), and spruce-balsam fir mixtures. The type is usually found on level to gently rolling sand plains, mainly of glacial outwash, fluvial, or lacustrine origin. It also grows on eskers, sand dunes, rock outcrops, ridges, and glacial lake beds and beaches.

Jack pine is a rather small, short-lived species that establishes readily on recently burned areas, especially on exposed sand sites. It is less shade-tolerant than any of its principal associates except quaking aspen and white birch. Thus, jack pine is a temporary type that on better sites is replaced by more shade-tolerant species when natural succession is not interrupted by fire. Fire encourages reproduction of jack pine at the expense of the more shade-tolerant species, except for oak and aspen, which sprout vigorously. On poor sites, such as light sandy soils where other commercial species do poorly, jack pine is more permanent. Here it tends to grow in pure stands but sometimes is mixed with northern pin oak. The poorest jack pine sites are largely free of shrubs; medium sites are characterized by low shrubs such as blueberry, sweet-fern, and dwarf-honeysuckle; and the better sites often have a dense undergrowth of American and/or beaked hazel, green alder, red-osier dogwood, and willows.

Evaluation and Discussion (see table 6)

Timber

Jack pine is one of the few species that is generally not re-established where it grows best. From a timber standpoint, it is desirable to convert good jack pine sites to the more productive red pine. Thus, the trend is to establish jack pine on dry soils where no other species fares as well.

The primary product objective for jack pine is to grow pulpwood, except on the better sites where intermediate thinnings are sometimes used to increase production of poles and small saw logs. Badly overstocked seedling and sapling stands may need thinning or cleaning to reduce the risk of stagnation.

Jack pine requires even-aged management; clearcutting followed by scarification or burning is best. Seedlings can be established by scattering

Table 6.—*Effects of some jack pine harvest options on forest resources—a desirability rating*[1] *(timber management objectives: pulpwood to a 3-inch top)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Even-aged management with clearcutting	40	1	U	0	0	+	U	+
		5	U	+	0	++	+	+
		20	++	+++	0	+	++	+
		50	+++	+++	0	+	++	+
	55	1	U	0	0	+	U	++
		5	U	+	0	++	+	++
		20	+	++	0	+	+++	+
		50	++	++	0	+	+++	+
	70	1	U	0	0	++	U	+++
		5	U	+	0	+++	U	+++
		20	+	++	0	++	+	++
		50	+	++	0	++	+	+
No harvest			0	0	0	U	+	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

cone-bearing branches, direct seeding, or planting. Shelterwood cutting is limited to stands that bear nonserotinous cones and where landscape and wildlife values are especially important.

Rotation lengths that maximize pulpwood yield range from 40 to 70 years, depending on stand density and risk from insects, disease, and weather. Generally, return on investment is greater with shorter rotations. Sawtimber and poles may require 70-year rotations.

Water

Comments for water in the red pine discussion (page 15) apply equally well to jack pine.

Wildlife

The jack pine type is generally beneficial to both edge and interior wildlife species. Its overall value to edge wildlife is less than that provided by the aspen or birch types, because jack pine itself is generally not as palatable and shrubs are not as prevalent. However, it is more valuable than the other conifer types, whose canopies intercept more light and thus lessen the development of lower vegetation layers. For wildlife sensitive to excessive snow depths, however, jack pine ranks lower than other conifers. The habitat provided by jack pine stands during the regeneration phase are most beneficial to edge wildlife, whereas older, more fully stocked stands tend to be more beneficial to interior species.

In general, management should favor maintenance of this type with a balanced distribution of age classes among stands (Ruske 1969). Most recommendations previously discussed for established red pine (pages 15-16) also apply to jack pine, except that, because jack pine is a short-rotation, intolerant type, a larger percentage of jack pine than red pine would be acceptable where intolerant types are in short supply.

The Kirtland's Warbler is an endangered species that nests in north-central Lower Michigan and requires breeding habitat that would not be met by following the general recommendations for red or jack pine. It breeds in young jack pine stands, usually of fire origin, which grow on the Grayling sand soil type. For nesting, stands should be 6 to 15 feet tall, well interspersed with small openings, and preferably larger than 200 acres. The requirement for small openings becomes more important with increasing stand age and density.

Visual Quality

Extensive areas of jack pine are considered by many people to be rather unattractive. Less extensive stands that lend diversity to the landscape or occur on rock outcrop ridges have high visual appeal.

Harvest options that include longer rotations or thinning and cleaning of excessively overstocked seedling and sapling stands will add to visual quality. Attention to size, close control of harvest, and use of appropriate techniques discussed in earlier sections will enhance the visual appeal of the type.

The no-harvest option will provide maximum visual quality from early maturity to stand break-up. On all but the poorest sites the no-harvest option will result in conversion to more tolerant species that may be even less visually attractive.

Diseases

Scleroderris canker causes a shoot dieback and stem canker on young jack pine. While the disease may act as a thinning agent in dense stands of reproduction, it can kill entire stands when severe. Older jack pine is also susceptible to the New York strain of *Scleroderris* canker mentioned for older red pine.

Eastern gall rust, sweet-fern rust, comandra blister, and stalactiform rust can damage jack pine of any age. The rusts are particularly capable of killing young trees. Older trees become badly malformed and are often not harvested. The cankers caused by these rusts can also allow entry of heart rot fungi.

Fomes pini and *F. pinicola* cause heart rot of mature and overmature jack pine. However, cull caused by these heart rots is seldom a problem for rotations as short as 70 years.

Armillaria pine rot and butt rot will infect jack pine, especially when the trees are established where hardwoods have been grown previously.

Davisomycella needle blight kills all but the current year's needles on infected jack pine. Severely infected trees might be killed, especially when young, but generally the disease only causes growth loss. Jack pine is also susceptible to *Diplodia* attack as mentioned for red pine.

Scleroderris canker and *Davisomycella* needle blight will reduce the visual quality of affected stands under the no-harvest option. The other diseases may actually be interesting to casual observers.

Insects

Although jack pine hosts a variety of insects that attack developing leaders during the establishment period, height growth is not seriously reduced and stem form, which is normally irregular, is not greatly affected. Saratoga spittle bug, however, can be a serious pest during the establishment period.

The most significant damage occurs during the pole stage when severe defoliation by the jack pine budworm and jack pine sawflies can kill suppressed trees and the tops of others. Budworm injury can be minimized by harvesting at a rotation age of about 40 years. Open-grown as well as very dense stands produce heavy crops of male cones, which enhance survival of jack pine budworm larvae.

SPRUCE-FIR

Type Description

The spruce-fir type occupies nearly 3 million acres in the Lake States. Despite the type name, balsam fir is typically more abundant within the type than is white spruce.

Spruce-fir is considered the climax forest type over a major part of the area occupied by aspen, birch, and associated conifer forests (Cooper 1913, Ohmann and Ream 1971). Old-growth stands have varying mixtures of balsam fir, white birch, and white spruce, with some black spruce, aspen, northern white-cedar, and occasional stems of black ash, red maple, and balsam poplar. Where succession is less advanced, white, red, and jack pine may be associated with the type. The type is sometimes represented by small (usually less than 10 acres), scattered stands of pure fir originating after fire, windstorm, or epidemics of spruce budworm (Roe 1950).

Over much of the Lake States balsam fir occurs as an understory within aspen, white birch, jack pine, white pine, and occasionally red pine types. In the natural course of succession, these types will eventually become spruce-fir as the overstory dies. Much of the spruce-fir type within the region originated in this manner, particularly areas that escaped disturbance for many years.

Spruce-fir stands will typically have a tall shrub layer composed of mountain-maple, hazel, and honeysuckle, and a poor low shrub layer, with mosses predominating over herbs as ground cover.

Evaluation and Discussion (see table 7)

Timber

From a silvicultural standpoint, spruce-fir is the most flexible of the eight types. It can be managed through either even-aged or uneven-aged systems, and in pure or mixed stands with aspen and birch. Even the crudest silvicultural prescriptions can provide good regeneration of balsam fir if a seed source is nearby. The only difficult and recurrent problem with the type is how to increase the proportion of white spruce, which has more value for high-quality paper and sawtimber.

Table 7.—*Effects of some spruce-fir harvest options on forest resources—a desirability rating*[1] *(timber management objectives: balsam fir pulpwood to a 3-inch top, and a white spruce sawtimber)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality	Edge species	Interior species	
Uneven-aged management with selection cutting	70	1	U	0	0	++	U	+++
		5	U	0	0	+++	U	+++
		20	+	0	0	+	+	++
		50	+	0	0	+	+	++
Even-aged management with clearcutting[2]	70	1	U	0	0	+	U	++
		5	U	+	0	++	+	++
		20	++	++	0	+	+++	+
		50	+++	++	0	+	+++	U
No harvest			0	0	0	U	++	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

[2] Clearcut width should not exceed 200 feet for natural regeneration.

Product objectives for this type are balsam fir pulpwood and white spruce pulpwood and sawtimber, with occasional yields of balsam fir sawtimber. Rotation ages should be approximately 70 years for fir and up to 90 for spruce where sawtimber is the objective. Little economic information is available for the spruce-fir type.

Even-aged management is particularly well-suited for mature or overmature even-aged stands. Clearcutting in narrow strips or small patches is best so that natural seeding can come from adjacent uncut stands. Large clearcuts should be avoided because they generally offer too harsh an environment for seeding establishment and the clearcut interior receives too little seed. Shelterwood cuttings also work well if a series of light cuts are conducted over a period of several years. Opening these old stands too quickly puts them in danger of windthrow. Once seedlings are established, the shelterwood can be removed completely. The shelterwood also allows larger areas to be regenerated at one time.

Uneven-aged management can be used in uneven-aged stands, or in young even-aged stands where the objective is to achieve uneven-aged structure. Single trees or groups of trees should be removed on 5- to 20-year cutting cycles as they mature, or in even-aged stands when the trees reach marketable size. Stands should be thinned at the same time to promote a good distribution of age and size classes. Uneven-aged management provides ideal regeneration conditions for the spruce-fir type.

Balsam fir often establishes in the understory of aspen and can be managed with it, either as an alternate crop in an even-aged system or as a concurrent crop in an uneven-aged system. In the even-aged system, the aspen is harvested when mature while the fir is still sapling or small pole size. Openings in the fir canopy will usually be large and numerous enough to allow scattered clumps of aspen suckers to be established. The fir is grown to maturity and the whole stand, fir *and* aspen, is clearcut. Aspen suckers will dominate the site, but in 10 to 20 years fir will re-establish in the understory. The success of this system depends on an adjacent fir seed source.

The uneven-aged aspen-fir system is much like the uneven-aged system for fir alone. Group selection of aspen and single-tree or group selection of fir will favor good regeneration of both.

Water

Comments under red pine (page 15) apply equally well to the spruce-fir type. In addition, since dense spruce-fir stands intercept more precipitation than pines (Helvey 1971), water yields from dense spruce-fir stands will be slightly less than from pine stands.

Wildlife

The spruce-fir community is generally beneficial to both edge and interior wildlife species. The generally dense tree canopy provides good winter cover. In stands with light to medium stocking and in those with an aspen component, the lower vegetative layer can be moderately well-developed and beneficial to edge wildlife. However, this layer is usually poorly developed and generally less valuable to edge wildlife than it is in the jack pine type.

As explained under the aspen type (page 9), McCaffery (1970) recommended that an area contain about 15 percent conifer cover to maximize wildlife production. Assuming that a management area contains about 15 percent spruce-fir, two silvicultural options could be pursued to maintain this proportion and enhance the type's value for edge wildlife. One would be to apply uneven-aged management through selection cutting on a cycle of 30 years or less to open the canopy and stimulate understory vegetation, while at the same time leaving portions uncut or lightly cut to retain some canopy cover. The other option would be to apply even-aged management that will balance age class distribution. Although Rutske (1969) recommended cutting in strips 65 to 100 feet wide or in small patches of about 0.5 acres for deer, strips up to 200 feet wide or patches up to 5 acres would also favor edge species. Cutting larger areas, progressive cutting, or two-stage, alternate-strip cutting in larger blocks would be more favorable for interior species.

Methods of increasing the acreage of spruce-fir include reserving from harvest stands likely to succeed to spruce-fir, or overstory removal in stands with a substantial spruce-fir understory. Decreasing the acreage of spruce-fir by conversion to aspen would most benefit edge wildlife species. This can best be accomplished in stands where enough aspen remains to provide a fully stocked sucker stand following clearcutting. Patches of 0.5 to 5 acres are recommended for most edge species, or even larger for moose.

Visual Quality

Except where it adds variety to the landscape, the type is not especially attractive. Where spruce-fir is extensive, small and medium-sized regeneration cuts may improve the overall visual appeal, especially if they open scenic vistas.

Selection cutting will maximize visual quality in stands that are not extensive. Aspen-spruce-fir management probably provides the greatest visual quality for the type.

The no-harvest option may maintain visual quality over limited areas, but salvage operations may be required periodically to remove windthrown, wind-broken, and insect-killed individuals. In spite of the abundant down and dead material, pristine vignettes displaying natural ecological processes have much appeal for some viewers—in this case, perhaps more philosophical than aesthetic.

Diseases

A number of diseases affect white spruce, but none is significant in its management. Balsam fir, however, is affected by several serious diseases.

Armillaria mellea causes a root and butt rot of balsam fir that is most severe where hardwood stumps remain from a previous forest.

Feather rot and balsam butt rot are the principal heart rot fungi responsible for nonutilization (cull) of balsam fir. Both of these fungi cause decay in the lower 12 feet of the first log.

Stereum sanguinolentum causes a heart rot of balsam fir. The fungus enters only through wounds, and therefore is most important in stands where uneven-aged management is practiced and in areas subject to ice storms.

Although *Armillaria mellea* will affect the visual quality of stands under the no-harvest option, none of the other diseases is important.

Insects

By far the most significant insect in the spruce-fir type is the spruce budworm; it is capable of causing widespread mortality. The balsam fir component is most severely damaged. Balsam fir generally will succeed itself in budworm-killed stands. However, the broken tops and snags persist for 10 to 15 years, and can provide fuel for fires and impede fire suppression efforts (Sando and Haines 1972). When fire follows spruce budworm outbreaks, succession tends to shift the composition toward other species. The spruce budworm is a natural component of the spruce-fir forest, and on a time scale of 50 to 100 years it assures ecological stability in the system (Baskerville 1975, Mattson and Addy 1975).

Mortality of balsam fir is increased when spruce is present in the stand, and is decreased when species mixtures not susceptible to budworm attack are present (Batzer 1969). Maintaining high stand density of fir also lessens the proportion of fir damaged. Injury to advance regeneration may be reduced by removing all mature host trees during clearcutting, since any residual mature spruce and balsam fir harbor the insects. When practical, partial cutting of balsam fir will reduce budworm damage in the residual stand (Batzer 1967).

BLACK SPRUCE

Type Description

The black spruce forest type occupies about 2.1 million acres of commercial forest land in the Lake States. Sixty-eight percent of this acreage is in Minnesota, and the remainder is in the northern parts of Michigan and Wisconsin. The black spruce type is a major resource for pulpwood in northern Minnesota. Christmas trees are harvested on a limited scale on sites too poor for growing pulpwood.

Black spruce grows in both pure and mixed stands; in some mixed stands it predominates, and in others it is important but not predominant, such as in the mixed swamp conifer, upland white spruce-balsam fir, and jack pine types.

The black spruce type is found mainly on organic soil in the Lake States, but it also occurs on mineral soil. Extensive areas of organic soil are found on gently sloping glacial lakebeds or smaller filled lakes associated with the Laurentian Shield, pitted outwash plains, and morainic areas. On both lakebed and filled-lake sites, the growth rate of black spruce is related to the surrounding ground water flow system. The best sites occur where the soil water is continuous with the regional ground water system and thus is enriched by nutrients flowing from mineral soil areas. The poorest sites occur where the soil water is "perched" above and thus is separated from this regional system. The fertility of these latter sites depends mainly on precipitation, which is relatively low in nutrients.

The growth rate of black spruce varies greatly; height of dominant trees at 50 years ranges from about 45 feet on the best sites to less than 15 feet on the poorest. Mature stands on good sites commonly yield 30 cords per acre for trees 3.6 inches d.b.h. and larger. In contrast, many stands on poor sites never produce merchantable pulpwood.

The black spruce type is common on mineral soil only in the Laurentian Shield area of northeastern Minnesota and in a few isolated areas of Upper Michigan. Here black spruce grows on gravelly and bouldery loam and on shallow soil over bedrock, where it usually is mixed with other species such as jack pine, aspen, and balsam fir, but occasionally forms a pure type. Growth is best where the slope is gentle and moisture is plentiful, either from a shallow water table or seepage. South of the Shield, black spruce is occasionally found on sandy soil with a high water table.

Black spruce stands on the best organic soil sites typically have a dense understory of tall shrubs such as speckled alder, willow, and red-osier dogwood. In contrast, stands on medium to poor sites are nonshrubby and have only some low shrubs such as Labrador-tea and leatherleaf. Sphagnum and feather mosses are common in nonshrubby black spruce stands. Pure black spruce stands on mineral soils are often characterized by poor development of shrub and herb components, but an extremely well-developed carpet of moss (Ohmann and Ream 1971).

Evaluation and Discussion (see table 8)

Timber

This discussion is limited to black spruce on *organic* soils. Black spruce is a fire type much like jack pine; much seed is stored in persistent cones, and becomes available for regeneration after fire. (The cones are not serotinous, however, and seedfall is dependable every year.) Thus, black spruce stands are initially even-aged but can eventually become uneven-aged as the stand matures and opens up, leaving openings for new regeneration. However, uneven-aged systems are neither optimal nor practical because they increase the risk of windthrow and infestation by dwarf mistletoe, and growth is less than in the full sunlight provided by even-aged systems.

Black spruce grows slowly, reaching merchantability in 60 to 150 years, depending on stand density. The highest rate of investment return and in many instances the only positive rate of return is obtained with short rotations on the better sites.

Table 8.—*Effects of some black spruce harvest options on forest resources—a desirability rating*[1] *(timber management objectives: pulpwood to a 3-inch top)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality[2]	Edge species	Interior species	
Even-aged management with clear-cutting	60	1	U	0	[0]	+	U	+
		5	U	0	[0]	++	+	+
		20	++	0	[U]	+	+++	U
		50	+++	0	[U]	U	+++	U
	90	1	U	0	0	++	U	++
		5	U	0	0	+++	+	++
		20	+	0	[U]	+	++	+
		50	++	0	[U]	U	++	+
	150	1	U	0	[0]	++	U	+++
		5	U	0	[0]	+++	+	+++
		20	U	0	[0]	+	++	++
		50	+	0	[0]	U	++	+
No harvest			0	0	0	U	+	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

[2] Assumes winter logging on frozen organic soils.

[ ] = Local increases in streamwater phosphorus concentration on brushy sites. Not significant unless tree harvesting is on a massive scale.

Because the trees are small and the fiber makes a high-quality paper, pulpwood is the only practical management objective.

Clearcutting, followed when needed by prescribed burning to control brush and dwarf mistletoe and to prepare the seedbed, is the best way to regenerate black spruce. If clearcuts are small or in narrow strips, natural seeding from adjacent mature stands is sufficient. Direct seeding can be used in large clearcuts. Shelterwood or seed-tree methods have the same disadvantages as uneven-aged management and are not recommended. Thinning to control stand density is not considered economical and is not practiced. Release by aerial herbicide spraying is recommended where immature spruce is severely suppressed by shrubs or hardwoods.

Water

Black spruce stands occur mostly on organic soils with high water tables. In these situations harvesting does not affect annual water yields, although minor effects can be measured. Clearcut areas will have slightly higher water tables than mature forests during wet periods and slightly lower water tables during dry periods. At the extremes, water tables may be about 2½ inches higher and 5½ inches lower. The effect on annual streamflow is balanced out.

Clearcutting black spruce on the more productive organic sites will increase nutrient concentrations in streamflow until an effective shade-producing canopy reappears. Nutrient increases are most dramatic when air temperatures exceed 80°F. Increases in phosphorus concentrations may be desirable or undesirable when they reach lakes. Phosphorus is a limiting nutrient in most lakes, so some increase may stimulate desirable levels of algae and fish production. Excessive increases in phosphorus, however, may promote undesirable algae blooms and fish die-offs. On a practical basis it would take massive cutting of black spruce on organic soil to affect downstream lake productivity in a measurable way.

Wildlife

The simple structure of black spruce stands provides little habitat for edge wildlife species. The best habitat is found in the early regeneration stages, in lightly stocked stands, and where black spruce is mixed with intolerant species on mineral soils. Even in these instances, however, suitability for edge wildlife is comparatively low and transitory. Black spruce provides mediocre habitat for a few interior species.

Where black spruce makes up about 15 percent of the management area (the amount of conifer cover recommended by McCaffery (1970), edge wildlife will benefit most from even-aged management. Clearcutting in blocks of about 5 acres or secondarily in strips up to 220 feet wide is recommended. Cutting larger areas, progressive strip cutting, or two-stage, alternate-strip cutting in blocks would tend to favor interior species. Where conifer stands are in short supply and the more beneficial conifer types (jack pine and northern white-cedar) are unsuited to the site, black spruce can be increased by reserving from harvest stands likely to succeed to black spruce, and by removing the overstory in stands with a substantial black spruce understory. Decreasing the acreage of upland black spruce would be most beneficial to wildlife if stands with mixed intolerant species were clearcut in blocks.

As ruffed grouse do with aspen, spruce grouse use several age classes of black spruce. Thus, harvest should be spaced over time and the areas well distributed, with first priority given to partial harvesting of extensive even-aged stands.

Visual Quality

Extensive areas of black spruce may have little visual appeal, but smaller acreages where the type adds to the diversity of the landscape or occurs as a fringe around bogs have high visual quality. Where the type occurs around bogs, a tamarack component frequently grows at the fringe, providing a very pleasing contrast of colors in the fall.

Mature black spruce stands with 80 to 150 square feet of basal area and little or no undergrowth except for a well-developed moss layer have high visual appeal.

Where stands are not extensive, the no-harvest option will maximize visual quality, primarily between maturity to stand break-up. After about age 70 butt rot increases, and after age 100 windthrow due to the rot becomes common. Excessive windthrow tends to diminish visual quality.

Major infections of eastern dwarf mistletoe generally reduce visual quality under any management option. However, minor infections produce curiosities (witches' brooms) that can have positive visual effect. In extensive areas of black spruce, even major infections may have a positive visual impact by opening small vistas to break the monotony.

Diseases

The most important disease of black spruce over any rotation length is eastern dwarf mistletoe. Dwarf mistletoe is a plant that grows on black spruce branches, obtains water and nutrients from the spruce, and causes witches' brooms, stunted growth, and sometimes death of the tree. A leaflet on how to identify and control mistletoe is available from the North Central Station on request (Ostry and Nicholls 1976b).

Root rots caused by *Armillaria mellea, Coniophora puteana, Polyporus schweinitzii, P. tomentosus,* and *Stereum abietinus* are major contributors to windthrow in black spruce, but wind alone, because of the shallow root system, can cause much uprooting. Although these rot fungi invade the butt log of black spruce, they do not cause significant cull.

Insects

Swamp black spruce is damaged little by insects even though the dense tree crowns may harbor a large variety of them.

NORTHERN WHITE-CEDAR

Type Description

The northern white-cedar type occupies 1.9 million acres of commercial forest land in the Lake States. The most extensive stands are in Michigan, which has 62 percent of the type's acreage. The remainder occurs in the northern parts of Minnesota and Wisconsin.

The white-cedar type is an important but greatly underutilized resource for both timber products and wildlife habitat. It produces large amounts of posts, poles, fencing, and lumber in certain localities of Upper Michigan, northern Minnesota, and northeastern Wisconsin. Present production of white-cedar pulpwood is minor, but the potential is substantial. The type also has great value for winter deeryards because northern white-cedar is highly preferred by white-tailed deer for shelter *and* browse. Although the extensive yards of Upper Michigan are particularly important, numerous smaller yards throughout the northern Lake States are vital during severe winters.

Northern white-cedar grows in both pure and mixed stands; in some mixed stands it predominates, and in others it is important but not predominant, such as in the mixed swamp conifer, black spruce, tamarack, and black ash-American elm-red maple types.

The northern white-cedar type is found primarily on organic soil in the Lake States, but it also occurs on mineral soil, mainly on seepage areas and limestone uplands. Growth is usually faster on mineral soil, and best on sites that are calcareous and moist but well-drained. Growth rate varies greatly; height of dominant white-cedar trees at 50 years ranges from at least 40 feet on the best sites to less than 15 feet on the poorest. Mature, fully stocked stands of pure white-cedar (at least 80 percent) on good sites commonly yield 50 cords per acre for trees 5 inches d.b.h. and larger. Much of this volume is in logs and poles, whereas many stands on poor sites produce only small posts.

Organic soil origin, degree of decomposition, and drainage in the upper horizons are good guides to site productivity, whereas soil depth is a poor guide by itself. The best soils are neutral or slightly alkaline and contain moderately to well-decomposed organic matter derived from woody plants or sedges. However, the upper 4 inches on these sites may be poorly decomposed sphagnum or other mosses. The best sites have moving soil water and are usually near streams or other drainageways. In contrast, the poorest sites have poorly decomposed acid soil derived from plants such as sphagnum moss throughout the whole root zone. These sites have little water movement (except during snowmelt) and are often far from drainageways.

Typically the tall shrub layer is well-developed, with species composition variable, depending on whether the stand is on organic or mineral soil. The low shrub layer is usually poorly developed, and the herb layer is also sparse. Mosses predominate over herbs in the latter, especially on organic soil.

Evaluation and Discussion (see table 9)

Timber

Because little management information is available for upland stands of northern white-cedar, the timber discussion is restricted to *swamp* stands.

This type is important for timber and winter deeryards, thus management decisions should attempt to accommodate both. Timber management objectives are to grow posts, poles, and sawtimber.

Even-aged management is recommended for regenerating northern white-cedar. Small clearcut patches or strips less than 200 feet wide are best for natural seeding from adjacent, uncut stands. Shelterwood cuts should be used to regenerate stands with no adjacent seed source.

Thinnings down to 150 square feet basal area per acre will remove undesirable hardwoods and tamarack (which have no shelter value for deeryards), as well as promote growth on crop trees. Rotation lengths vary from 80 to 145 years, depending on site and product objective.

Water

Comments for black spruce (page 25) apply equally well to northern white-cedar on organic soils. On mineral soils, dense stands of northern white-cedar have interception losses similar to those of dense spruce-fir stands.

Wildlife

The white-cedar community provides habitat for many edge and interior wildlife species. The dense tree canopy and tall shrub layer provide important winter food and cover for deer, and to a lesser extent for snowshoe hare. However, the importance of white-cedar stands to deer in winter depends on severity of weather and availability of other suitable conifer types. For snowshoe hare, other conifer types are probably more important.

Because white-cedar is tolerant and long-lived, the type is likely to retain its current prevalence. However, regeneration may be difficult to obtain where deer are abundant. In stands of less than 200 acres, the impact of dense deer populations can be lessened by two-stage clearcuts. The objective is to remove all winter cover for deer during the critical regeneration period, especially where the

Table 9.—*Effects of some northern white-cedar harvest options on forest resources—a desirability rating*[1] *(timber management objectives: posts, poles, and sawtimber)*

Forest practice	Rotation length (years)	Size of harvest (acres)	Investment return	Water		Wildlife		Visual quality (landscape and on-site appeal)
				Yield	Quality[2]	Edge species	Interior species	
Even-aged management with clearcutting or two-stage shelterwood; timber emphasis on posts, poles, and sawtimber; wildlife emphasis on deer browse and shelter	25	1	U	0	0	++	U	+
		5	U	0	0	+++	U	+
		20	U	0	[U]	+	U	U
		50	U	0	[U]	+	U	U
	50	1	U	0	0	++	U	+
		5	U	0	0	+++	U	+
		20	+	0^3	[U]	+	U	+
		50	+	0^3	[U]	+	U	U
	80	1	U	0	0	++	U	++
		5	U	0	0	+++	U	++
		20	++	0^4	[U]	+	+	+
		50	+++	0^4	[U]	+	+	+
	120	1	U	0	0	+	U	+++
		5	U	0	0	+	+	+++
		20	++	0^4	[U]	U	++	++
		50	+++	0^4	[U]	U	++	+
	145	1	U	0	0	U	U	+++
		5	U	0	0	U	++	+++
		20	+	0^4	[U]	U	+++	++
		50	++	0^4	[U]	U	+++	+
No harvest			0	0	0	U	+	+++

[1] +++ = excellent; ++ = good; + = fair; 0 = no impact; U = unfavorable impact.

[2] Assumes winter logging on frozen organic soils.

[3] ++ on mineral soil areas with good drainage.

[4] + on mineral soil areas with good drainage.

[ ] = Local increase in streamflow phosphorus concentrations on brushy sites. Not significant unless tree harvesting is on a massive scale.

area is small and the density of deer high. This forces deer out of the area so that a new stand can be established. In large stands, cutting units can generally be made big enough to obtain adequate regeneration in spite of the deer by applying two-stage strip cuts in blocks of 40 to 160 acres (Verme 1965). In the first stage, alternate strips 66 to 100 feet wide are cut in a large block to initiate regeneration. The remaining strips are removed as soon as sufficient regeneration is obtained, thereby creating an essentially even-aged stand large enough to withstand the impact of deer browsing. However, if the potential exists for a rise in the water table or an increase in speckled alder, large clearcuts should be avoided.

In regions where the impact of deer on regeneration is not a problem, the size of cut is less important. In these instances, Rutske (1969) recommends reducing the cut to as little as 10 acres. Scheduling the harvest of white-cedar stands during the winter further benefits deer by providing browse (Verme 1961).

Little is known about the requirements of other wildlife inhabiting white-cedar stands. However, the silvicultural treatments dictated by the presence of high deer populations should benefit interior species.

Visual Quality

Extensive areas of the type are not very appealing, but limited areas add diversity to the landscape and provide an attractive fringe around lakes, bogs, and swamps. Stands with high basal area, large trees, and little undergrowth have the highest visual quality.

On good sites the no-harvest option provides higher visual quality from maturity to stand break-up than the harvest options because of the longevity of the species.

Diseases

Northern white-cedar is relatively disease-free, and none of its diseases should be a management problem under any of the options presented. Butt-rot fungi that cause a white, stringy rot (*Poria subacida*) or a brown, cubical rot (mainly *Polyporus balsameus* and *P. schweinitzii*) are common in mature trees on the drier lowland sites.

Insects

Although northern white-cedar is an occasional host to a number of leaf feeders and wood borers, the most significant damage results from galleries of carpenter ants (both red and black). Up to 20 percent of the stems in a stand may show loss in the lower 3 to 6 feet of the stem from the extensive nests of these insects (Graham 1918). Carpenter ants are also an important food of the pileated woodpecker. Mature stands are most affected by these insects.

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APPENDIX

Table 1.—Common and scientific names of species cited in text.

Common Name	Scientific Name
TREES	
American elm	*Ulmus americana*
Aspen (quaking)	*Populus tremuloides*
Balsam fir	*Abies balsamea*
Balsam poplar	*Populus balsamifera*
Bigtooth aspen	*Populus grandidentata*
Black ash	*Fraxinus nigra*
Black spruce	*Picea mariana*
Jack pine	*Pinus banksiana*
Northern pin oak	*Quercus ellipsoidalis*
Northern white-cedar	*Thuja occidentalis*
Red maple	*Acer rubrum*
Red oak	*Quercus rubra*
Red pine	*Pinus resinosa*
Tamarack	*Larix laricina*
White (paper) birch	*Betula papyrifera*
White pine	*Pinus strobus*
White spruce	*Picea glauca*
SHRUBS	
Alder	*Alnus* spp.
American hazel	*Corylus americana*
Beaked hazel	*Corylus cornuta*
Blueberry	*Vaccinium* spp.
Bush-honeysuckle	*Diervilla lonicera*

Cherry	*Prunus* spp.
Green alder	*Alnus crispa*
Labrador-tea	*Ledum groenlandicum*
Leather-leaf	*Chamaedaphne calyculata*
Mountain-maple	*Acer spicatum*
Red-osier dogwood	*Cornus stolonifera*
Speckled alder	*Alnus rugosa*
Sweet-fern	*Comptonia peregrina*
Willow	*Salix* spp.
Wintergreen	*Gaultheria procumbens*

LESSER PLANTS

Aster	*Aster macrophyllus*
Bracken fern	*Pteridium aquilinum*
False lily-of-the valley	*Maianthemum canadense*
Feather mosses	*Dicranum* spp., *Hylocomium splendens, Ptilium crista castrensis,* and *Pleurozium schreberi*
Sphagnum moss	*Sphagnum* spp.

DISEASE ORGANISMS

Armillaria pine root and butt rot	*Armillaria mellea*
Balsam butt rot	*Polyporus balsameus*
Brown cubical rot	*Polyporus schweinitzii*
Comandra blister rust	*Cronartium comandrae*
Davisomycella needle blight	*Davisomycella ampla*
Diplodia fungus	*Diplodia pinea*
Dwarf mistletoe	*Arceuthobium pusillum*
Eastern gall rust	*Cronartium quercum*
Feather rot (white stringy rot)	*Poria subacida*
Fomes heartrot	*Fomes pini*
Fomes root rot	*Fomes annosus*
Hypoxylon canker	*Hypoxylon mammatum*
Perennial canker	*Ceratocystis fimbriata*
Perennial canker	*Nectria galligena*
Phellinus (white) trunk rot	*Phellinus igniarius (=Fomes igniarius)*
Poria canker	*Poria obliqua*
Red pine needle case	*Lophodermium pinastri*
Red pine shoot blight	*Sirococcus stroblilinus*
Scleroderris canker	*Scleroderris lagerbergii*
Shepherd's crook shoot blight	*Venturia termula*
Stalactiform rust	*Peridermium stalactiforme*
Sweetfern rust	*Cronartium comptoniae*
White pine blister rust	*Cronartium ribiocola*

INSECTS

Aspen stem borers	*Saperda* spp., *Oberea* spp., *Agrilus* spp.
Birch skeletonizer	*Bucculatrix canadensisella*
Birch leaf miner	*Fenusa pusilla*
Black carpenter ant	*Camponotus pennsylvanicus*
Bronze birch borer	*Agrilus anxius*
European pine shoot moth	*Rhyacionia buoliana*
Forest tent caterpillar	*Malacosoma disstria*
Introduced pine sawfly	*Diprion similis*
Jack pine budworm	*Choristoneura pinus*
Jack pine sawflies	*Neodiprion pratti banksianae*, *N. swainei*
Large aspen tortrix	*Choristoneura conflictana*
Poplar borer	*Saperda calcarata*
Redheaded pine sawfly	*Neodiprion lecontei*
Red carpenter ant	*Camponotus ferrugineus*
Saratoga spittlebug	*Aphrophora saratogensis*
Spruce budworm	*Choristoneura fumiferana*
White grubs	*Phyllophaga* spp.
White pine weevil	*Pissodes strobi*

Table 2.—Some representative edge and interior wildlife species found in the aspen, birch, and associated conifer forest types of the Lake States.

MAMMALS

Edge species	
Beaver	*Castor canadensis*
Black bear	*Ursus americanus*
Bobcat	*Felis rufus*
Deer mouse	*Peromyscus maniculatus*
Eastern chipmunk	*Tamias striatus*
Fisher	*Martes pennanti*
Least chipmunk	*Eutamias minimus*
Masked shrew	*Sorex cinereus*
Moose	*Alces alces*
Short-tailed shrew	*Blarina brevicauda*
Snowshoe hare	*Lepus americanus*
Southern red-backed vole	*Clethrionomys gapperi*
White-tailed deer	*Odocoileus virginianus*
Interior species	
Marten	*Martes americana*
Red squirrel	*Tamiasciurus hudsonicus*
Northern flying squirrel	*Glaucomys sabrinus*

BIRDS

Edge species

American robin	*Turdus migratorius*
American woodcock	*Philohela minor*
Black-capped chickadee	*Parus atricapillus*
Boreal chickadee	*Parus hudsonicus*
Broad-winged hawk	*Buteo platypterus*
Chestnut-sided warbler	*Dendroica pensylvanica*
Chipping sparrow	*Spizella passerina*
Common flicker	*Colaptes auratus*
Common redpoll	*Acanthis flammea*
Kirtland's warbler	*Dendroica kirtlandii*
Least flycatcher	*Empidonax minimus*
Ovenbird	*Seiurus aurocapillus*
Pine siskin	*Carduelis pinus*
Purple finch	*Carpodacus purpureus*
Red-breasted nuthatch	*Sitta canadensis*
Red-eyed vireo	*Vireo olivaceus*
Ruffed grouse	*Bonasa umbellus*
Song sparrow	*Melospiza melodia*
Yellow-bellied sapsucker	*Sphyrapicus varius*

Interior species

Bald eagle	*Haliaeetus leucocephalus*
Bay-breasted warbler	*Dendroica castanea*
Blackburnian warbler	*Dendroica fusca*
Black-throated green warbler	*Dendroica virens*
Canada warbler	*Wilsonia canadensis*
Cape may warbler	*Dendroica tigrina*
Gray jay	*Perisoreus canadensis*
Magnolia warbler	*Dendroica magnolia*
Nashville warbler	*Vermivora ruficapilla*
Osprey	*Pandion haliaetus*
Pileated woodpecker	*Dryocopus pileatus*
Ruby-crowned kinglet	*Regulus calendula*
Saw-whet owl	*Aegolius acadicus*
Spruce grouse	*Canachites canadensis*
Tennessee warbler	*Vermivora peregrina*
Veery	*Catharus fuscescens*
White-throated sparrow	*Zonotrichia albicollis*
Yellow-rumped warbler	*Dendroica coronata*

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Ohmann, L. F., H. O. Batzer, R. R. Buech, D. C. Lothner, D. A. Perala, A. L. Schipper, Jr., and E. S. Verry.

1978. Some harvest options and their consequences for the aspen, birch, and associated conifer forest types of the Lake States. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-48, 34 p. North Cent. For. Exp. Stn., St. Paul, Minnesota.

Describes some harvest options and their consequences in terms of timber investment return, water yield and quality, wildlife, visual quality, and disease and insect impact for the aspen, white birch, red pine, white pine, jack pine, black spruce, spruce-fir, and white-cedar forest types of the Lake States.

OXFORD: (908 & 911 & 187)— (77). KEY WORDS: Even-aged management systems, uneven-aged management systems, visual quality, wildlife, water quality.

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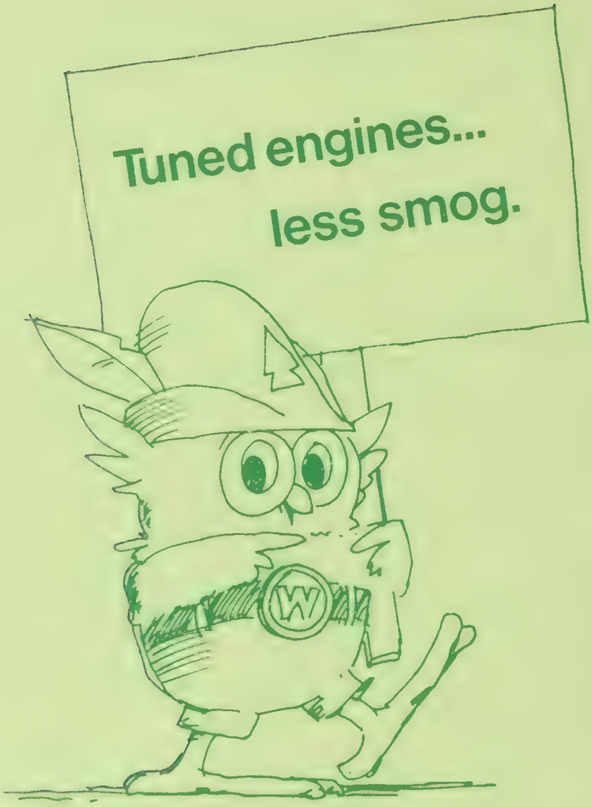
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A GENERALIZED FOREST GROWTH PROJECTION SYSTEM

Applied To

The Lake States Region

Central Forest Experiment Station
st Service, U.S. Department of Agriculture

PREFACE

The papers presented here describe a new computerized system developed to project forest growth and mortality with or without tree cutting for any mix of species or stand structure encountered in the field.

Growth and mortality coefficients have been developed for the forests of the Lake States Region, and the system has been used to update forest inventories, identify silvicultural treatment opportunities, and project long-run timber output and growth response. The system is designed to be used as the core of a larger Forest Resources Evaluation Program (FREP) being developed by the North Central Station, but it has potential for much wider use.

Work to enhance and refine the system's capabilities is continuing, and further progress has been made since these papers were prepared for publication. Interim modules to account for regeneration and for tree cutting to meet timber product removal objectives have been added. Although the capabilities of the projection system are changing rapidly we thought it appropriate to publish these papers to give a snapshot picture of its development as of September 1977.

ARNE K. KEMP
Assistant Director
North Central Forest Experiment Station

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North Central Forest Experiment Station
Robert A. Hann, Director
Forest Service - U.S. Department of Agriculture
1992 Folwell Avenue
St. Paul, Minnesota 55108
1979

FOREST RESOURCES EVALUATION SYSTEMS—A NEEDED TOOL FOR MANAGING RENEWABLE RESOURCES

Allen L. Lundgren, *Principal Economist,*
and **Burton L. Essex,** *Principal Resource Analyst*

The Forest and Rangeland Renewable Resources Planning Act of 1974 requires the Secretary of Agriculture to prepare a Renewable Resource Assessment for the Nation every 10 years, and a long-range Renewable Resource Program for the Forest Service every 5 years. The first assessment and program were published in 1976 (USDA Forest Service 1976a, 1976b). The second assessment is scheduled to be made during 1979, with a second program document based on this assessment due in 1980. These resource assessments provide the basis for national programs, but also can serve as guides for framing regional resource policies and programs.

State land management and planning agencies require resource assessments at the state and local level for long-range resource planning and development. River basin and other special-area planners need resource inventory information for political subdivisions updated to a common base year.

Large individual private and public forest properties and management units likewise need resource evaluation systems designed to project prospective supply and demand from their properties, and to identify and evaluate potential management opportunities.

NORTH CENTRAL'S RESPONSIBILITY

The North Central Forest Experiment Station of the Forest Service, U.S. Department of Agriculture, has the responsibility for conducting statewide forest resource inventories and regional resource assessments within the North Central Region of the United States. To meet these and other needs expressed above, the Station must have the capability to acquire, process, and evaluate information about the current and future extent, condition, and use of the renewable resources within the Region. An evaluation system must be designed specifically to fit the existing data base and data analysis capabilities already existing for this Region. This system must be usable for regional, State, and local assessments as the need arises, and be compatible with any national assessment system developed.

WHAT SHOULD A RESOURCES EVALUATION SYSTEM DO?

Obviously, we need an evaluation system that can, using basic forest resource inventory and other data available for a resource area, project future forest resource supply and demand for the area, and evaluate potential alternative resource management programs designed to change supply or demand. Such a system or series of systems should be able to evaluate timber, wildlife, recreation, water, forage, and special uses of the forest resource and their interactions from an ecologic-environmental, economic, and socio-cultural point of view. There is little doubt that such a resource evaluation system must be computer-based if it is to handle the large amount of information and analytical procedures necessary for regional assessment.

The dimensions of this job are enormous. They include economic, ecologic-environmental, and socio-cultural evaluations of the following resource use systems: timber, wildlife, recreation, water, forage, and special uses (fig. 1). For each resource

Type of Evaluation	Resource Use System					
	Timber	Wildlife	Recreation	Water	Forage	Special uses
Ecologic						
Environmental						
Economic						
Social						
Cultural						
Legal						

Figure 1.—*Potential dimensions of a forest resources evaluation program.*

use system we must obtain and organize the physical and biological information needed for evaluation, and develop methods for doing this within reasonable cost and time constraints. We also must develop and apply methods for evaluating economic and social costs and benefits of defined alternatives. Substantial work is needed to determine the nature and extent of interrelations among the various resource use systems so that these can be considered in evaluating opportunities and making regional assessments. These analyses should be made for the different resource components, resource owners, owner organization levels, and resource users (both direct and indirect), and for different spatial and temporal extents. They also should recognize the degree of uncertainty regarding our knowledge.

Because the existing forest resource is usually in a condition far from ideal, such an evaluation system must be capable of dealing with the resource situation as it exists on the ground. It must be able to handle the entire range of sites and stand conditions, all levels of tree stocking, cull and sound trees, and almost every conceivable mixture of tree species and sizes. It must be able to produce both short- and long-run projections of resource conditions for a wide range of potential management treatments within an acceptable level of accuracy. Further, it should be able to handle the other components of forest ecosystems besides trees in order to cover all forest uses.

EXISTING SYSTEMS ARE INADEQUATE

A forest growth projection system capable of handling the complexities of the real world in enough detail to evaluate alternative stand treatment programs has not been available in the past. Individual growth and yield models have been developed, but mainly for pure stands of single species or for a few types under limited conditions. These, however, have proven to be inadequate in dealing with the mixed ages, sizes, and species, the non-normal stocking, or the high proportion of cull trees that often typify existing stands. Because each model was developed independently, using different kinds of inputs and producing different kinds of output, attempts to incorporate them into a comprehensive analytical system have not been successful. Also, since no growth and yield models exist for many forest types and stand conditions, any system developed from existing models would be, at best, incomplete.

It is doubtful that a comprehensive system capable of conducting integrated multi-resource, multi-use, multi-objective evaluations simultaneously will be successfully developed in the near future. Rather than wait until a complete system is developed, the North Central Station has decided to develop parts of the system now. Since much work already has been done on the timber resource, developing a computerized system to evaluate the timber resource in economic terms was chosen as a logical first task. Later, other resource components will be linked to timber.

WHAT'S THE FIRST STEP?

As a first step in meeting the need for a regional forest resource assessment system, we are developing a computerized timber resource projection and evaluation system that will update and project timber inventories and product yields, determine the extent of potential stand treatment opportunities, and evaluate from an economic standpoint potential programs to increase future timber supplies. Figure 2 shows the major components of this system that require development. Each of these components in turn includes subcomponents that will require considerable research.

THE GROWTH PROCESSOR— NUCLEUS OF THE RESOURCES EVALUATION SYSTEM

Basic to this timber resource evaluation system is a subsystem to project future stand development in response to proposed management activities. To be useful for regional analyses, such a forest growth projection system must handle all forest conditions encountered in forest inventories. In short, it must be a generalized forest growth projection system.

This growth projection system must project future forest growth on forest inventory plots so they can be updated to any given base year. To do this adequately it must account for growth on all trees inventoried, mortality, recruitment or ingrowth of new trees, and removals of trees through cutting. It must cover the entire range of site and stand conditions encountered.

This growth projection system also must project the response of individual stands or classes of stands to prescribed treatments, such as precommercial thinning, partial cutting, and cull-tree removal, so treatment opportunities can be evaluated. When fully developed, it will also be used to estimate potential yields from fully-stocked stands to establish the potential productivity of specified sites. Such a system is basic to many types of timber resource evaluations.

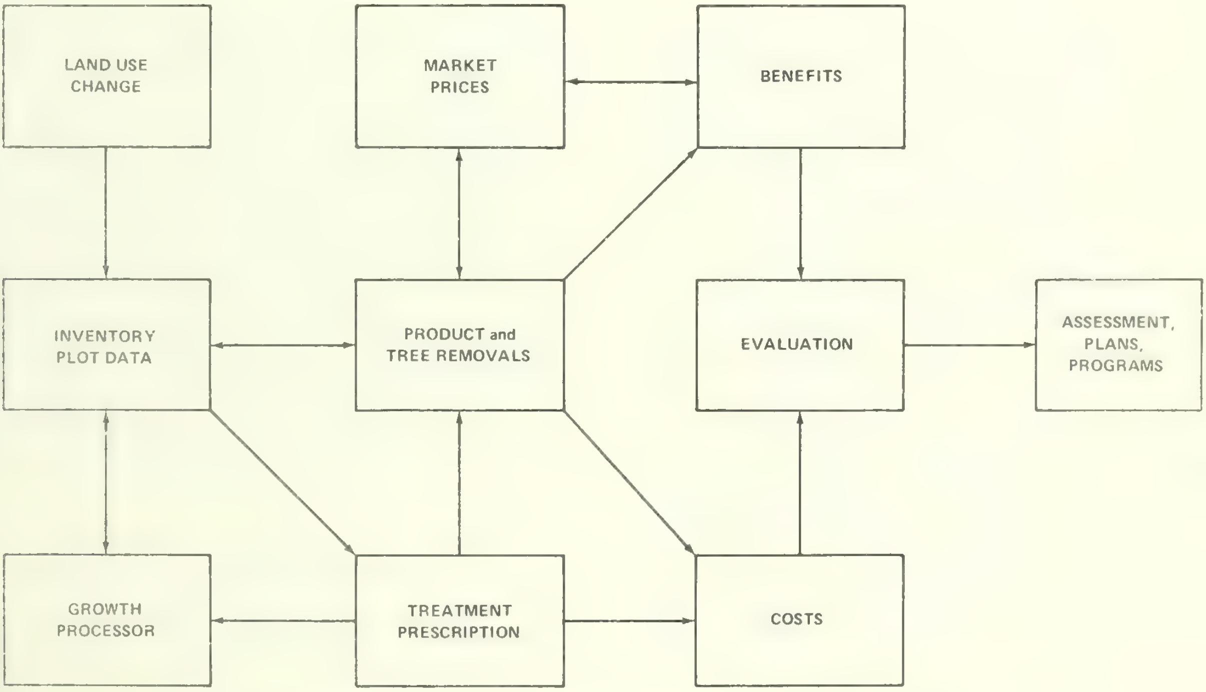

Figure 2.—*Major components of a timber resource evaluation system for economic analysis.*

NORTH CENTRAL'S APPROACH

In recognizing the need for a new approach to this problem, researchers at the North Central Forest Experiment Station have developed a computer-based, generalized forest growth projection system that can be used as the basis for a timber resource evaluation system. The details of this system are summarized in the papers that follow. Although the system is still under development, it already can project short-run growth responses in enough detail to be useful in evaluating treatment alternatives in many stands. With further development it will provide the basis for a timber resource evaluation system for regional forest resource assessments.

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USDA Forest Service 1976b. RPA: A recommended Renewable Resources Program. 648 p. plus Appendices. Washington, D.C.

DESIGN

Rolfe A. Leary, *Principal Mensurationist*

A major new direction is surfacing in the development of forest growth models. The trend is away from single-species models toward models sufficiently general to handle any pure or mixed stand of any structure and density on any site. This paper explains the design features of a generalized forest growth projection system that can be used for short- to medium-range projections of existing stands. The details are found in other chapters of this report.

Development of mathematical equation models of forest growth has been an active area of mensuration research for the past 40 years. One of the early studies reported was that of MacKinney *et al.* (1937). In the early work, goodness of fit of model to data was the primary discriminating variable in model selection. Grosenbaugh (1958) developed this to a highly detailed state. Little consideration was given to generality or theorification potential. Most models applied only to pure stands of a single species with relatively simple stand structures. The last 5 to 10 years have seen many efforts to develop growth models general enough to handle a variety of conditions (Fries 1974). The models for some species are quite detailed, giving a high resolution level, but other models, especially for economically unimportant species and mixed stands, are still at low resolution levels. Several approaches (e.g., Stage 1973, Ek and Monserud 1974, Hegyi 1975, and probably others[1]) have been developed and are being improved and extended to cover additional forest conditions.

DESIGN OBJECTIVES

I had two fundamental objectives in designing the model part of this growth projection system. The first was to capture, to the degree possible, the "essence" of the process of stand growth and development. Thus, I sought a structural similarity between the model and the forest stands. The second objective was to accomplish the first objective as efficiently as possible.

From the standpoint of modeling, a forest stand can be viewed as a set of interactive, differential energy transformers and accumulators (Leary 1970b). Thus, to model forest stands, one must deal effectively with these five key concepts: (1) set, (2) interactive, (3) differential, (4) transformer, and (5) accumulator. Nearly all models address these concepts, although they may be given different names or not be identified explicitly.

From "set" we know we are dealing with an aggregate of individuals; from "interactive" we know the individuals in the aggregate are interacting; from "differential" we know that not every individual in the set is the same; from "transformer" and "accumulator" we know that the individuals are both factory and warehouse. If we can develop a mathematics that will address each of the concepts and synthesize them into a whole, we may have some structural similarity between model and nature.

My preference was to look first to "transformer" and "accumulator" when shopping for a mathematics to use. This nature-based constraint on our shopping list directs us to differential equations. For the sake of simplicity we go to first-order ordinary differential or difference equations. Here we see the symbolic expression of this ideal:

$$\frac{dY}{dt} \text{ or } \frac{\Delta Y}{\Delta t} = f(Y,...)$$

---

[1] *Arney, J. S. 1977. Personal communication. Centralia, Washington.*

Verbally these symbols are saying: "that which results from growth is itself typically capable of growing". It is important to understand that Y is the dependent variable in this equation and t the independent. Persons accustomed to using regression methods sometimes have difficulty, especially with the differential equation form, because the dependent variable, Y, is on both sides of the equality.

Once having made the critically important choice of a mathematics to use, we can proceed to examine the possibilities for dealing with "set", "interactive", and "differential". The concepts of set and differential are complementary in the following way: from set we easily consider subsets, but not just any subsets. They should be structured in a way so the individuals within a subset are similar and those between subsets are different. Subsetting or stratifying an aggregate is a natural way to formalize differentia. Thus, the union of concepts "set-subset" and "differential" suggest that we may need as many Y's as we have subsets. We turn, of course, from scalars to vectors to accommodate this need. The result, in terms of a symbolic expression of our ideal, is now only slightly altered:

$$\frac{dY1}{dt} \text{ or } \frac{\Delta Y1}{\Delta t} = f(Y1, Y2, \ldots)$$

$$\frac{dY2}{dt} \text{ or } \frac{\Delta Y2}{\Delta t} = f(Y2, Y1, \ldots)$$

These equations must be solved together because they are coupled or simultaneous equations. We see that the mathematics of differential/difference equations is so well-suited to our problem that in the handling of "set-subset" and "differential" we have also dealt with the concept of "interactive".

The practicing forester often considers "stand" through more operational concepts: (1) structure, (2) density, (3) species composition, (4) site, and (5) stand history. How does the mathematics we have selected allow us to account for these important aspects of "stand"? The later sections of the paper go into the details of this question, so here I will only indicate their general occurrence in the above equations.

$$\frac{\Delta Y1}{\Delta t} = f(\text{density, site, stand history,...})$$

$$\frac{\Delta Yn}{\Delta t} = f(\text{density, site, stand history,...}).$$

↑ STRUCTURE ↓

SPECIES

↑ COMPOSITION ↓

Thus, we see that density, site, and stand history are dealt with by making them arguments in the right-hand side of a difference equation. Stand structure and species composition are accommodated by changing the number of simultaneous equations.

An important operational advantage made possible by our choice of the mathematics of difference equations is the ease with which resolution level may be handled. The next few sections of the paper are organized around the concept of resolution level. They reflect the current design state, and are in part chronological because a conscious method used was one suggested by Polya (1945): take an insoluble (but apparently simple) problem and embed it into a larger problem so as to create a class of problems. The reasoning is that the solution to the larger class of problems may be more obvious than the solution to the one simple problem.

For example, the potential choices of a model for a single-species stand with unimodal diameter distribution are numerous. Generalization to handle mixed stands with varying stand structures and densities is possible with some and not with others. This eliminates a large fraction of the candidate models. Other forms are eliminated by applying the reverse process, and assessing the ability to reduce or collapse the complicated model to a simple form for simple stands and less precise estimates. The result of this process is a tremendous reduction in the number of feasible models that can make up the core of a generalized projection system capable of variable resolution levels.

HOW THE PROJECTION SYSTEM WORKS

Like any system, the workings of the projection system may be broken up into three parts: input, output, and transformation or internal workings.

Part	*Form*
input	a list of interacting trees showing species, d.b.h., and crown ratio[2] for each tree.
output	a list of trees showing species, new d.b.h. and new status if tree is a mortality tree.
transformation	a stand component change equation, an allocation rule, and a mortality function.

Input and Output

The input list must identify each tree's species and d.b.h. and hopefully its crown ratio. Although many temporary inventory procedures do not record trees in this detail, it is possible to fabricate a tree list from a stand table that would, if summarized, produce the stand table. Crown ratio is collected by the national Forest Survey, but by few others. This important, although usually missing, input variable has been successfully approximated through a simple relation between mean crown ratio and 10-year mean basal area density (Holdaway *et al.* 1979). We use crown ratio as an indicator of stand history. It helps to tell us whether a stand with 80 square feet of basal area grew up from 40 square feet or was cut back from 160 square feet.

Output from the projection system is a new set of d.b.h. values for the trees which survived the projection interval and a status change from live to dead for all trees projected to die.

Although the input tree list is aggregated to form initial conditions for the system, the tree list is not discarded. This would be throwing away information. Instead, it is carried along and updated every year or periodically. This greatly facilitates a flexible output of information. The job of summarizing the output tree list is thereby separated, as it should be, from the job of summarizing the input tree list and growing the stand. Output tree list diameter class breakdowns should not be forced on the projection system. They are normally based on technology and economics, and are of no value in projection.

Transforming Input to Output

The mathematical model for transforming the input tree list to an updated output tree list has four parts: potential function, modifier function, allocation rule, and mortality function.

The first two parts fit together as shown below:

$$\left[\begin{array}{l}\text{One year change}\\ \text{in sum of tree}\\ \text{diameters for a}\\ \text{given number}\\ \text{of trees}\end{array}\right] = \left[\begin{array}{l}\text{potential yearly}\\ \text{d.b.h. growth}\\ \text{for a tree}\\ \text{with mean}\\ \text{crown ratio}\\ \text{and dbh on a}\\ \text{given site}\end{array}\right] \cdot \left[\begin{array}{l}\text{number}\\ \text{of trees}\end{array}\right] \cdot \left[\begin{array}{l}\text{fraction of the}\\ \text{potential growth}\\ \text{actually}\\ \text{occurring}\end{array}\right]$$

In symbolic equation form the relationship is:

$$\frac{\Delta Y}{\Delta t} = [PDG] \cdot [NT] \cdot [MODIFIER] \qquad (1)$$

The potential function is designed to estimate how rapidly the mean tree would be growing in d.b.h. if it were not interacting with any other trees (Hahn and Leary 1979). The potential growth is multiplied times the number of trees, giving a potential change in sum of diameters for NT trees. The modifier function reduces the potential change to what has been observed from permanent growth plots (Leary and Holdaway 1979). In somewhat more detail, and with a slightly changed notation, equation (1) is:

$$\frac{\Delta Y}{\Delta t} = [f_1(\overline{D},\overline{CR},SI)][NT][f_2(Y,NT)], \qquad (2)$$

where:
f_1 is the potential function,
f_2 is the modifier function,
$\overline{D}$ is mean d.b.h.
$\overline{CR}$ is mean crown ratio,
SI is site index,
Y is sum of tree diameters, and
NT is number of trees.

The allocation rule disaggregates the projected growth put on by NT trees, $\Delta Y/\Delta t$, to the individual trees on the input tree list. The simple rule:

$$\left[\begin{array}{l}\text{percent of } \Delta Y/\Delta t\\ \text{that should be given}\\ \text{to tree } i\end{array}\right] = f\left[\begin{array}{l}\text{percent of growing}\\ \text{stock represented}\\ \text{by tree } i\end{array}\right] \qquad (3)$$

has proven to be a useful point of beginning for this task (Leary, *et al.* 1979).

The mortality rule takes the allocated d.b.h. growth for each tree and, using an appropriate function, computes a probability of death for a tree of that species growing at the allocated rate (Buchman 1979). Equation (4) shows this basic relation:

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[2] *Crown ratio is the ratio of full live crown length to total tree height.*

$$\begin{bmatrix}\text{Probability of}\\ \text{death for } i^{\text{th}}\\ \text{tree of species } j\end{bmatrix} = f\left[\begin{pmatrix}\text{allocated d.b.h.}\\ \text{growth for previous}\\ \text{period}\end{pmatrix}, \ (\text{species})\right] \cdot (4)$$

The computed probability is compared with a pseudo-random number drawn from a uniform distribution on the interval [0,1]. If the random number is less than the computed probability, the tree is called a mortality tree, and its status changed to reflect this. It does not enter further in the projection computations.

Once the mortality has been specified and the tree list otherwise updated, it is again summarized for input, and equations (2), (3), and (4) are executed to project another year's growth. The entire process is repeated over and over again as many times as the user desires.

Throughout this discussion it has been implicit that all trees in the stand would be grouped together and projected with a single equation. Thus, at this level of resolution the model is at the stand model end of the stand model-tree model continuum of growth models.

In moving away from the stand model we go to stand component models, wherein groups of trees in the stand are projected with different equations. The key to this flexibility lies in the use of simultaneous equation models and in the particular form of the modifier function. The potential function, allocation rule, and mortality functions are little affected as resolution level is changed.

LOW RESOLUTION MODEL STRUCTURE

When the projection system is operating at a low resolution level, the input tree list is summarized into two or more groups called components. For this discussion we assume that tree species is the breakdown criterion. If one has, for example, a two-species mixture, the input tree list is summarized into two components. Each component is projected by one of a system of two simultaneous equations as follows:

$$\Delta Y1/\Delta t = \begin{bmatrix}\text{Potential d.b.h.}\\ \text{growth of mean}\\ \text{tree of first species}\\ \text{as a function of}\\ \overline{D}_1, \overline{CR}_1 \text{ and } SI_1\end{bmatrix} \cdot \begin{bmatrix}\text{number of}\\ \text{trees of}\\ \text{first species}\end{bmatrix} \cdot \begin{bmatrix}\text{fraction of potential}\\ \text{that first species}\\ \text{attains due to pres-}\\ \text{ence of trees of}\\ \text{species one and}\\ \text{species two}\end{bmatrix} (5)$$

$$\Delta Y2/\Delta t = \begin{bmatrix}\text{Potential d.b.h.}\\ \text{growth of mean}\\ \text{tree of second}\\ \text{species as a}\\ \text{function of}\\ \overline{D}_2, \overline{CR}_2 \text{ and } SI_2\end{bmatrix} \cdot \begin{bmatrix}\text{number of}\\ \text{trees of}\\ \text{second}\\ \text{species}\end{bmatrix} \cdot \begin{bmatrix}\text{fraction of potential}\\ \text{that second species}\\ \text{attains due to pres-}\\ \text{ence of trees of}\\ \text{species two and}\\ \text{species one}\end{bmatrix}$$

$\Delta Y1/\Delta t$ is disaggregated to trees of the first species using a species-specific allocation rule, and $\Delta Y2/\Delta t$ to trees of the second species. Mortality probabilities are computed with species-specific coefficients in the mortality equation. An updated tree list is then ready to be summarized again and projected for another period.

Let us go back and take a closer look at the modifier function, since it, of all parts of the model, is changed the most. The functional form of the modifier used to date has been:

$$[1-e^{\beta/f(Y,NT)}] \cdot \tag{6}$$

The form in (6) is used when the model is for a single species, hence has a single equation—the lowest resolution level possible. Here β represents how the species interacts with itself in a pure stand. When going to a mixed stand, β is not changed, but the denominator of the exponent is, as follows:

$$\frac{\Delta Y1}{\Delta t} = [PDG_1]\ [NT_1] \left[1\text{-}e^{\beta_1/(f_1\ (Y1,NT_1) + \omega_1 f_2\ (Y2,\ NT_2, Y1,\ NT_1))}\right]$$

$$\frac{\Delta Y2}{\Delta t} = [PDG_2]\ [NT_2] \left[1\text{-}e^{\beta_2/(f_1\ (Y2,NT_2)\ +\ \omega_2 f_2\ (Y1,\ NT_1, Y2,\ NT_2))}\right], \tag{7}$$

where

- β_1, β_2 represent how species one and two, respectively, affect themselves when growing in pure stands,
- f_1, f_2 are functions of sum of diameters (Yi) and number of trees (NT_i) of the species being projected, and
- ω_i are the coefficients that tell how species two affects species one (first equation) and species one affects species two (second equation).

If $\omega_1=1$, this indicates that species two affects species one the same as species one affects itself. A similar interpretation may be given to $\omega_2=1$. The specific forms of the functions f_1 and f_2 in equation (7) are discussed in detail elsewhere (Leary and Holdaway 1979).

INTERMEDIATE STRUCTURE

Intermediate level models differentiate not only by species but also by size within species. Thus, the input tree list is partitioned by size class within species. How do we incorporate size of tree into the model?

There are three separate but related aspects to this question. One has to do with the mechanism by which the model handles size in addition to species. The second aspect deals with the class movement problem — the movement of trees from one size class to another. The third deals with choosing class bounds for aggregating the input tree list.

The first aspect is easily handled because the model form is such that equations may be added to the system to project size classes within species. When this is done the denominator of the exponent in the modifier function is more complex, but the potential function, allocation function, and mortality function remain essentially unchanged. The modifier function for the first equation would take on a form such as:

$$1-e^{\beta_1/(f_1\,(Y1,NT_1) \,+\, \omega_{11}\, f_2\,(Y2,NT_2,Y1,NT_1) \,+\, \omega_{12}\, f_3\,(Y3,NT_3\,Y1,NT_1) \,+\, \ldots)} \qquad (8)$$

The denominator of the exponent of e thus has the form of a linear combination of interaction coefficients and functional relations between the component being projected and all other components. This pattern of relations (8) is repeated for each size class within each species, that is, for each equation in the system.

The second aspect, how to move trees from one class to another, is dealt with by keeping all trees in the class to which they were initially assigned. Since the trees in a class are growing, the attributes of the class change over time, rather than the trees changing classes. Two substantial benefits result from this approach: (1) Because trees do not change classes, summaries of permanent growth plot data do not have discontinuous trends caused by trees growing into and/or out of a class. The summaries, such as basal area in a class at several points in time, show fairly continuous changes. This allows modern calibration methods to be used to estimate the β and ω values (Leary 1970a, 1970b, 1972, 1975; Leary and Skog 1972). (2) Computational efficiencies are gained in the projection process itself since it is not necessary to check the correctness of class assignment as the trees' diameters are increased. An added benefit is that the user has the choice of not applying the allocation rule-mortality submodels every year, rather only when output is desired.

The third aspect is treated by partitioning the list of trees of each species into relative size groupings rather than into size groupings set on a cardinal scale of numbers. If, for example, we use two size equations for each of two species, the d.b.h. class limit might be such that a predetermined percent of the trees are larger than the limit and the rest smaller. By using this relativistic approach when calibrating the modifier function, each equation of the simultaneous system is assured of having trees present in the class it represents. In using the model for projection, we avoid the computational inefficiencies incurred when many equations (size classes) have no trees in them. Of course, mortality or partial cutting could cause some of the relativistic classes to have few, if any, trees, but this can always be rectified by reallocating the trees to the classes.

The increased precision that occures from adding more size equations is not known at this time. It is anticipated that three equations per species will meet many needs.

The allocation rule works as before except that the percentages are based on each component-that is,

$$\left[\begin{array}{l}\text{percent of } \dfrac{\Delta Y12}{\Delta t} \\ \text{that should be} \\ \text{given to tree } i\end{array}\right] = f \left[\begin{array}{l}\text{percent of growing} \\ \text{stock in component 1,2} \\ \text{represented by tree } i\end{array}\right] \qquad (9)$$

Again, the workings of the mortality submodel are unaffected by resolution level. It functions the same as for the simplest model.

HIGHEST RESOLUTION MODEL STRUCTURE

Let's skip now to the highest resolution level that this model can produce. It is attained when the number of simultaneous equations is increased until each tree is in a class by itself, hence projected by a separate equation. In this way it is clear that there is a continuum of growth models from stand (all trees in one class) to tree (one tree in each class).

In going to the highest resolution level the basic model structure is the same:

$$\frac{\Delta Y_k}{\Delta t} = [PDG_k]\,[1$$

$$\left[1\text{-}e^{\beta/(f_1\,(Y_k) + \sum_{j=1} \omega_j f_2\,(Y_k,\ Y_j,\ x_k - x_j,\ y_k - y_j))}\right].(10)$$

Here the denominator of the exponent of e has the same formulation as many individual tree growth models. Y_k is now the diameter of the subject tree with spatial coordinates x_k,y_k. The neighborhood trees are of diameter Y with spatial coordinates x_j,y_j. The function f_2 characterizes the competition factor common to these formulations.

The potential function now predicts the maximum d.b.h. growth of a single tree with diameter Y_k, crown ratio CR_k, on site, SI. The allocation rule is no longer needed because in equation (10) tree *i* is 100 percent of change as well as growing stock. It can be retained, however, by making the functional relation in (9) the identity relation. The mortality function and relation operate normally, giving an estimate of the probability of death based on $\Delta Y_k/\Delta t$ rather than the disaggregated growth given by the allocation rule.

EFFICIENCIES OF THE DESIGN

Efficiency of the design may be viewed from a number of perspectives. Consider the following:

(a) Efficiencies in modeling are permitted by breaking the overall problem into smaller, semi-independent parts.

When the overall model is decomposed into the potential, mortality, and modifier functions, and an allocation rule, efficiencies result because all but one can be separately completed prior to a synthesis of the parts. Team efforts need this parallelism. The relation of the jobs to each other and to the data base is shown in figure 1 for the present, nearly parallel effort, and for a hypothetical serial effort. Figure 1a shows that only the modifier function development is dependent on completion of another part before it can be totally completed. This allows a rapid updating of coefficients in all models once a new or updated calibration data base is available. It also minimizes the amount of work needed to recover from errors. Figure 1b shows a serial or cumulative type of model development. This approach has two major disadvantages: submodel 4 cannot be completed until submodel 3, and so on, and an error in submodel 1 requires changes in submodels 2, 3, and 4 as well as in itself. Both of these disadvantages relate to the speed with which work can be accomplished. Models of a serial or cumulative nature are best constructed by one person.

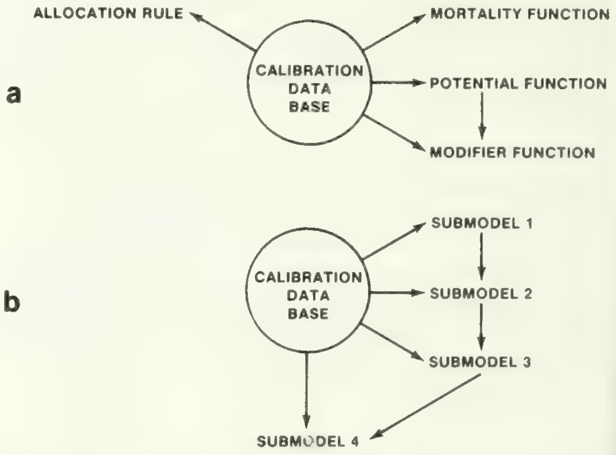

Figure 1.—*(a) Relation between data base and submodels for current design showing a nearly parallel structure. (b) Relation between data base and submodels for a hypothetical design showing a serial structure.*

(b) Efficiency is related to use of information in the calibration data base.

Recall that a design feature of the model calls for each tree to be assigned to a particular class and to remain in that class, and for the size distribution of trees to be partitioned so that about the same number of trees is in each class. When these two features are combined it is possible to use a multipoint boundary value problem approach to the estimation of the modifier function. The source of efficiencies here is that a boundary value approach does not require the taking of differences, often over uneven time intervals (see table 2, Christensen *et al.* 1979). Numerical analysts caution against taking differences of a noisy signal because doing so accentuates the noise relative to the true signal. The regression approach, wherein differences are taken, admittedly used in the potential, mortality, and allocation rule, ignores this caution. Keeping a small noise-to-signal ratio is very important in regions of the country where forest growth rates (i.e., signal strengths) are relatively low.

When the input tree list is partitioned by absolute size class limits, for example, 4.0-5.9, 6.0-7.9, etc., in a stand table projection, numerous stands to be projected may have no trees in the upper or lower classes. When the input tree list is partitioned on a percentile basis, each size class is certain of having a number of trees present. This ensures that the calibration data base information available to develop the projection equation coefficients is used on every plot. Figure 2 compares the traditional stand table and relativistic approach to tree list partitioning.

(c) Efficiency is related to simplicity of the mathematical equations.

When using differential/difference equations such as dY/dt or $\Delta Y/\Delta t = f(Y)$ to explain a pattern of Y over time, also given by $Y = g(t)$, the rule is that f is algebraically simpler than g. In fact, quite simple functions, f, can produce an extremely varied pattern of Y values over time. The use of systems of difference equations to handle the process complexity introduced by mixed tree sizes and species helps to keep the right-hand side of each equation as simple as possible.

(d) Efficiency is gained by building into the model the response to treatment.

The particular form of the right-hand side of the difference equations helps answer the question of stand response to a treatment calling for tree removals. This is made possible by having an upper limit of component change, given by the product of potential growth and number of trees, and a modifier of the upper limit, expressed as a function of stand density. The modifier has a form such that as density increases by growth, the value of the modifier decreases, but if density is abruptly decreased by cutting or mortality, the modifier is increased (fig. 3).

(e) Efficiency of computations must also be considered.

Here the concern is the number of arithmetic operations that must be performed per unit of output information; for example, an updated tree list. The multiple resolution level design feature is responsible for most of the gains here. If one wishes, the number of equations may be reduced to one (for a pure stand), and the tree list diameters updated every 10 years rather than every year. Doing this would have an effect on the precision of estimates of future forest conditions, but it would materially reduce the computational load to produce an updated tree list. The trade-offs between computational load and precision of estimates have not been thoroughly examined at this time.

(f) Efficiency in computer hardware requirements should be a part of the design.

The design of this projection system is such that one is not restricted to either a large storage capacity or extremely fast digital computer. Storage requirements can be reduced by such measures as:

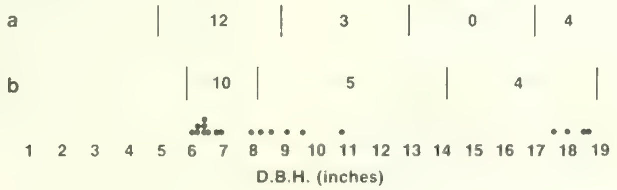

Figure 2.—*(a) The traditional (metric) approach to partitioning a sample distribution of trees. Notice that the 12.9-16.9-inch class has no trees. (b) The relativistic approach to tree list partitioning used in this Design. For illustration the groupings are nearly ½, ¼, ¼*

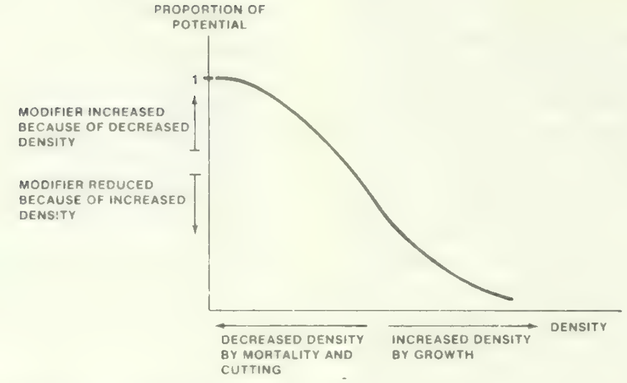

Figure 3.—*Relation between changes in the proportion of the potential change, increased density due to growth, and decreased density due to mortality and cutting.*

(1) projecting shorter tree lists (i.e., smaller plots), and (2) using lower resolution levels. Execution times can be reduced by employing both of these measures and by updating tree diameters and estimating mortality every 10 or so years (rather than every year). By a judicious combination of measures to reduce both storage and execution time requirements, it is anticipated that the projection system can be made to function on both full-size and mini-computers.

DIMENSIONALITY

The fundamental premise in calling the higher dimensional models higher resolution models is based on the reduction in heterogeneity within class as class "width" is reduced. Theoretically, as heterogeneity is reduced, ability to predict growth is increased. In a practical sense, however, the increased predictability may not be a linear function of number of classes (equations). In other words, going from a single equation for a two-species mixed stand to two equations may increase precision 20 percent, but adding two more equations may not increase precision another 20 percent. We are confronted with the costs of calibrating and using whatever resolution level is developed. The determination of an optimum resolution level for growth modeling seems analogous to finding optimum sampling intensities wherein sampling intensities have precisions and costs associated with each.

The use for which a growth projection system is intended, it has been argued, determines the resolution level at which one should operate. Another consideration is the following relation between dimensionality of the model (equivalent to my resolution level) and the time horizon over which projections are to be made:

$$\mathrm{d}=\mathrm{f}\left(\frac{1}{h}\right) k_{\mathrm{a}} \qquad (11)$$

where h is the time horizon over which projections are to be made,
d is the dimension of the model state vector,
k_{a} is a constant for a given accuracy or precision level, and
f is a function (Kahne 1976).

For simplicity's sake, if f is assumed the identity function the relation is:

$$\mathrm{d}=\frac{k_{\mathrm{a}}}{h} \qquad (12$$

Thus, the model dimension should be reduced for long-range projections and increased for short-range projections, to give the same level of accuracy.

The relation in equation (11) is apparently well-accepted by scientists involved in large-scale modeling. In general, however, it is not accepted by scientists working in forest projection. Too often projections are made for any time horizon of interest without regard to the dimensionality of the model. Sometimes single tree models have given unreasonable values after projections for 100 or 200 years, and this fact has been used to discredit the entire approach. On the other hand, stand (single equation) models cannot be used for short-term evaluations of tree spacing relationships, and this fact has been used to criticize this well-established approach. Obviously there are needs requiring growth projection systems with a spectrum of resolution levels.

In theory, it seems reasonable that one should be able to go from one resolution level to another without having to calibrate the denominator in the modifier function for every level. One would, of course, have to calibrate at several, say three, levels, but from then on one would simply input to the system the resolution level a user desires or can afford. The modifier function, as well as the other parts, would be computed by interpolation or extrapolation from the three calibrated levels.

USE ENVIRONMENTS

Once the initial calibration of the projection system has been completed there are at least three types of environments in which it may be used. One environment is where the objective is simply to project plot tree lists to a future time. This input-transformation-output schema is shown in figure 4. The algebraic forms come from the design phase, coefficients come from the calibration phase, and the input tree list may come either from temporary or permanent forest plots. No projection system should be used in this manner for prolonged periods of time without also being used in the second environment.

In the second environment accuracy and precision of the projection system are evaluated. The schema for this environment is shown in figure 5. Here, in addition to input tree list, projection system, and output tree list, I have added the "experience", detector and controller parts to the schema. This environment requires that permanent forest growth plot data be used for the input tree list and that, after a number of years has elapsed, a remeasurement of the plots be made and used as "experience". A comparison of the difference is the function of the detector, which passes the distribution of differences back to a controller, which uses it to modify the algebraic forms and coefficients in the projection system.

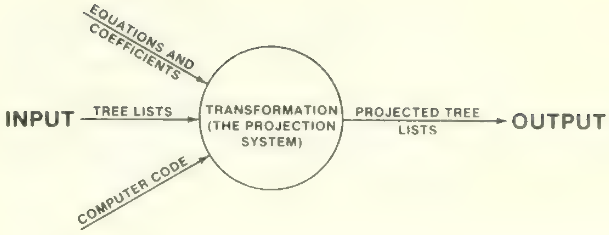
EQUATIONS AND COEFFICIENTS
INPUT
TREE LISTS
TRANSFORMATION (THE PROJECTION SYSTEM)
PROJECTED TREE LISTS
OUTPUT
COMPUTER CODE

Figure 4.—*Schema of environment for unverified projections.*

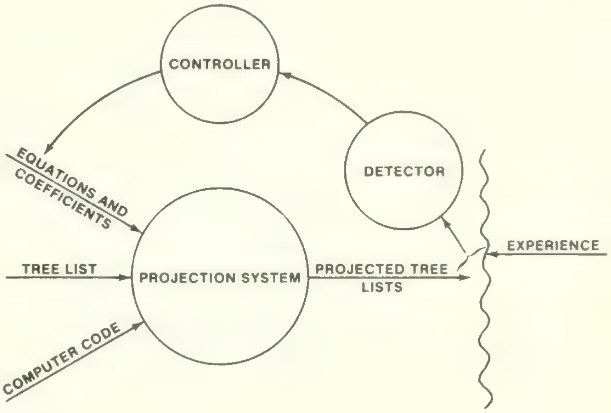

Figure 5.—*Schema showing processor in a cybernetic system involving use of permanent forest growth plots to correct the processor.*

Reason suggests that with an untested projection system one should not wait too long for another measurement — an "experience" reading. It also suggests that when little deviation is detected after such a reading one may want to project for a longer period before the next check is made with "experience". Under conditions where exogenous variables are thought important, for example, climatic variations, it may be desirable to both fix an upper limit to the projection period and automatically use the most recent "experience", in place of the most distant, to recalibrate the model. This would produce a running average type model, as opposed to a cumulative model wherein all past measurements are included in the calibration data base.

A third use environment is shown schematically in what I have called the scenario environment (fig. 6). Here, the projection system is instructed to execute various management recommendations and guides, and the outputs of each set, each scenario, are examined in light of various performance indices.

SUMMARY

Forest growth and yield research appears to be entering a new era where mathematical models are evaluated for generality of applicability as well as the traditional goodness of fit of equations to data. The basic model structure discussed in this paper is shown to be adaptable to single equation models as well as to models with large numbers of simultaneous equations. By using a relativistic approach to size class assignment the approach is made more computationally efficient than when fixed-diameter intervals are used. The concept of calibrating three resolution levels of the model and computing the needed coefficients in other resolution levels is presented, as is the notion that length of projection period should determine dimensionality of the model. Variable resolution level, relativistic models will be more easily tailored to the individual needs and budgets of users than are today's models.

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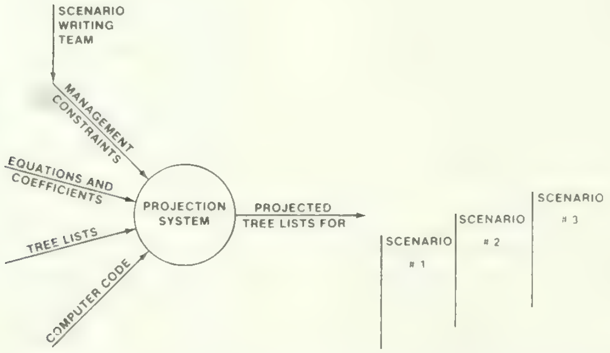

Figure 6.—*Schema of scenario environment. The growth processor is used to produce alternative output vectors for the inputs selected by the scenario writing team.*

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DATA BASE

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Jerold T. Hahn, *and* **Rolfe A. Leary,**
Principal Mensurationists

The need for growth projection systems that apply to all forest conditions of an ownership has been emphasized by Lundgren and Essex (1979), and a candidate projection system has been described by Leary (1979). Others have been described by Ek and Monserud (1974), Hegyi (1975), and Stage (1973). All the descriptions make it clear that a satisfactory model will not be developed by analyzing a few growth plots. Rather, we need to have available a large amount of data. The data base for the current study covers 44 different studies in Minnesota, Wisconsin, and Michigan. Included are 1,501 plots containing 484,574 individual tree measurements on 92,649 trees.

The purpose of this paper is to describe the data base used to calibrate the growth projection system from several perspectives: space, time, age, site, and species. The data base used to validate the model is presented in Leary *et al*. (1979) and the data needed to implement the model are described in Hahn and Brand (1979).

SOURCES OF DATA

Calibration of the growth projection system requires permanent growth plots with individual tree records at several points in time. Our sources were plot records from (1) cutting experiments, (2) demonstration woodlots, (3) industrial continuous forest inventory, and (4) personal records of forest growth. In each case, the growth information came from permanent sample plots, rather than complete forest enumeration. The plots were all fixed size—either circular or square. Square plots varied from 0.1 to 0.5 acre, and circular plots varied from 0.1 to 0.2 acre. In some cases only trees greater than 9 inches d.b.h. were measured; for others all trees greater than 0.6 inches d.b.h. were measured. Some plots were located randomly or systematically throughout the forest lands of an ownership. Other plots, coming largely from experimental forests, were all from similar quality sites.

Measurement data from five properties were supplied to us on magnetic tape, and data from five other properties were supplied on cards. The data from the remaining 34 properties were supplied on the original field data collection forms. Inconsistent form layout between studies added considerably to the work of preparing field sheets for direct keypunching. Data transcribing was avoided as much as possible.

During 1975 and 1976 each plot was visited and one or more of the following variables was measured or estimated: d.b.h., crown class, crown ratio, and tree status. These data were added to the already existing data.

DISTRIBUTION OF DATA SOURCES

The spatial distribution of the data sources is shown in figure 1. Lower Peninsula of Michigan data are entirely from plantations of red and jack pine. Wisconsin data are mostly from natural stands of hardwoods—oak-hickory type in the south and west, and northern hardwoods in the north—and northern white-cedar. The two Wisconsin plantation studies are Star Lake red pine adjacent to Michigan and white spruce near the Menominee Reservation. The northern Minnesota studies include natural and plantation studies of red pine and jack pine, and natural stands of quaking aspen, white pine, and black spruce.

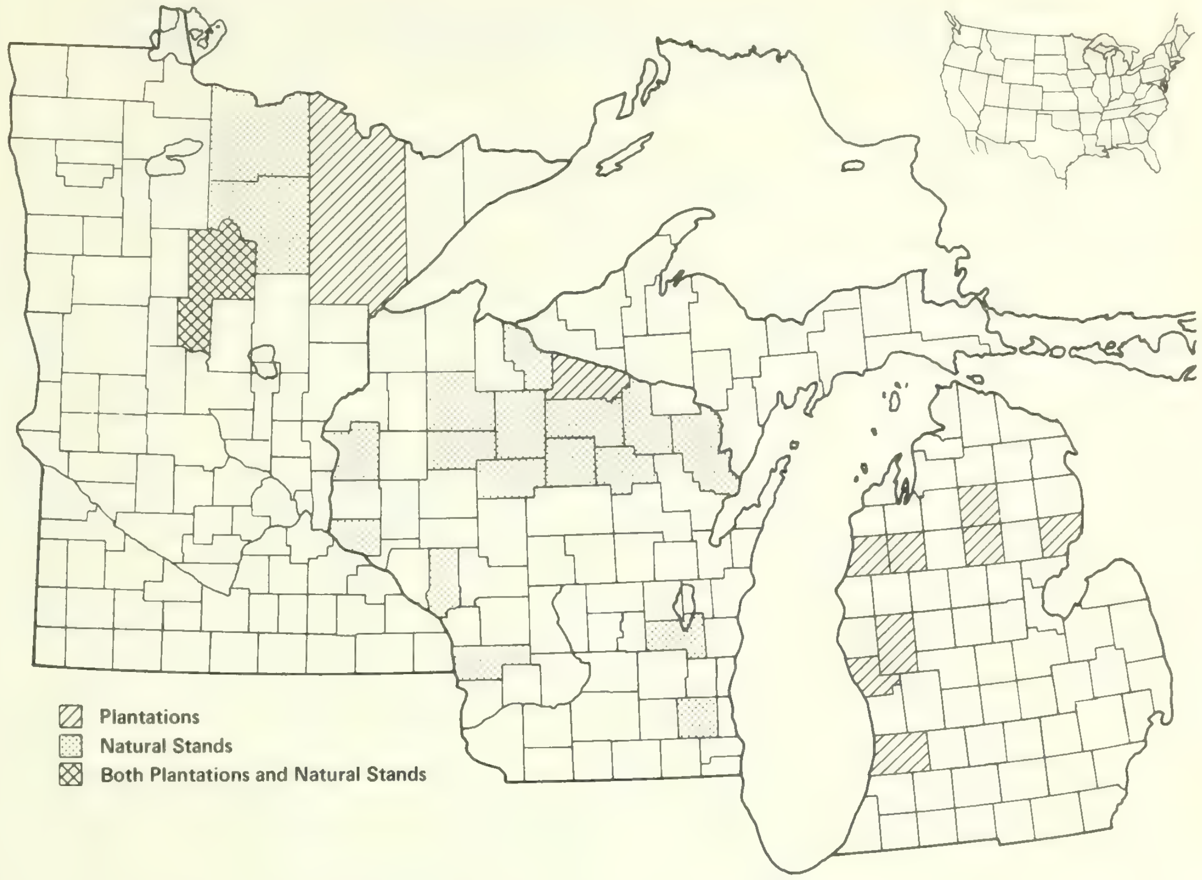

Figure 1.— *Location of counties with one or more calibration data sources in Minnesota, Wisconsin, and Michigan.*

The distribution of data sources by 1977 age (time) and site (matter/energy) is shown in table 1. Each age-site table is for a different forest type. Although the total number of plots in table 1 is 1,501, 1,529 plots were available for use; however, the variable necessary for determining forest type was not available on 28 plots. The stand age at which plot measurements were used may be as much as 20 to 30 years less than the ages given in table 1. For example, the 26 jack pine plots in the 31-40 (age)-50 (site index) cell were 36 years old in 1977. They had, however, been measured since 1953 (table 2), so the measurements began when the trees were 12 years old.

The distribution of the data sources by starting date and elapsed time between measurements is shown in table 2. The oldest measurements were made in 1938, giving nearly 40 years of observations. Others are not far behind at 30+ years of records. Not every plot on a property was measured where an "X" occurs in table 2.

PROCESSING AND STORING DATA

Information on field sheets was either keypunched directly or transcribed to 80-column sheets and then keypunched. The card data, as well as all data from magnetic tapes, were put into a standard format on disk files for editing. Following correction of all apparent data errors, the edited data were joined with the following information and placed in a master format:

(1) Mode of stand origin, treatment, replication, property number, plot number.
(2) Site index, site index species, and year of stand origin for up to five species per plot.
(3) Soils information.
(4) Forest type.
(5) Denominator of plot size fraction.
(6) Number of trees on plot.
(7) Number of measurements in time.

Table 1.— *Distribution of 1,501 permanent forest growth plots used for model calibration by age and site within 13 forest types in the Lake States (Site class 30 ranges from 25 to 34, 40 from 35 to 44, etc.)*

JACK PINE

Age class	Site index class								Total
	30	40	50	60	70	80	90	100	
21-30		1			1				2
31-40			26		1		1		28
41-50				1	65				66
51-60				1					1
61-70		62							62
Total									159
SWAMP CONIFER									
31-40					1				1
41-50			1						1
51-60		1	1						2
Total									4
TAMARACK									
21-30				1					1
71-80		1							1
81-90	2								2
Total									4
NORTHERN WHITE CEDAR									
31-40					1				1
61-70		1							1
71-80	1								1
91-100	1	20							21
100+	1								1
Total									25
OAK-HICKORY									
31-40					1	1			2
41-50			1		2	2			5
51-60		1		1	4	3			9
61-70					26	2			28
71-80			1		3				4
81-90		1	1	1	10				13
91-100			6	22	1				29
100+			11	40	15	1			67
Total									157

RED PINE

Age class	Site index class								Total
	30	40	50	60	70	80	90	100	
0-20						1			1
21-30					1	3		1	5
31-40					39	1			40
41-50				2	1				73
51-60		14	18		1				33
61-70			47		63				110
81-90			18						18
91-100				1					1
100+			149	14					163
Total									457
WHITE SPRUCE-BALSAM FIR									
0-20			1						1
21-30			1	1		1			3
31-40			2	6	3		1		12
41-50			1	5	2	1			9
51-60		1	1	5	11	1			19
61-70		1		21	3				25
71-80	1								1
Total									70
LOWLAND-HARDWOOD									
41-50				1					1
51-60	1	1							2
61-70					1				1
71-80		1							1
100+	1		2						3
Total									8
QUAKING ASPEN									
0-20		1	1						2
21-30		1	2	2	1	1			7
31-40		6	2	5	1		1		15
41-50		2	6	6	3	1			18
51-60		2	2	6		28	1		39
61-70		1		6	7				14
71-80			2						2
Total									97

WHITE PINE

Age class	Site index class								Total
	30	40	50	60	70	80	90	100	
0-20			1		1				2
21-30		1							1
31-40			1						1
41-50				4	2				6
51-60			1		1	1			3
61-70					3				3
71-80					10				10
91-100				17					17
100+				27					27
Total									70
BLACK SPRUCE									
21-30			1	2					3
31-40	1			1					2
41-50	12	1	3		1				17
51-60	1		1						2
61-70			2	1					3
100+		1							1
Total									28
NORTHERN HARDWOODS									
0-20		1							1
21-30			1	2	2		1		6
31-40		2	1	5	5				13
41-50		2	6	11	20	2			41
51-60			7	14	2	37			60
61-70	1	1	6	31	112	9			160
71-80		2	9	3	39				53
81-90		2	1	1	14				18
91-100		1	1	17	3				22
100+		2	27	4	3	4			40
Total									414
PAPER BIRCH									
21-30		1							1
31-40				1					1
41-50		1		2	1				4
61-70			1						1
91-100				1					1
Total									8

Table 2.—*Distribution of permanent growth plot measurements after the earliest measurement for calibration data base from Michigan, Wisconsin, and Minnesota.*

PROPERTY/STUDY	MAJOR SPECIES	YEAR OF EARLIEST MEASUREMENT	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
MICHIGAN																																						
NC-40 (Wellston)	Jack pine	53	X					X	X	X	X	X				X				X	X			X	X													
NC-178 (Crawford Co.)	Jack pine	60			X	X												X																				
NC-43[illegible] (Bosom Field)	Red pine	52			X	X	X			X	X	X				X	X				X	X	X	X		X	X											
NC-433 (Buck Creek)	Red pine	51			X	X	X		X	X	X	X			X	X	X			X	X	X			X	X	X											
NC-434 (Croton Dam)	Red pine	52				X			X		X					X					X					X												
NC-436 (Ravenna)	Red pine	60				X	X		X	X						X	X																					
NC-437 (Sooner)	Red pine	60		X			X										X																					
WISCONSIN																																						
Apple River THF	Oak, White pine	47						X		X		X				X													X									
Argonne THF	Northern hardwoods	47	X	X	X	X	X	X	X	X			X				X	X				X	X					X										
Cairns THF	Northern hardwoods	49				X				X				X					X								X											
Ellsworth THF	Northern hardwoods	48					X						X		X					X								X										
Chilsen THF	Hemlock, Yellow birch, Maple	47		X	X	X	X		X		X			X				X	X	X								X										
Dundee THF	Red oaks, Northern hardwoods	47			X				X			X					X												X									
Hardies Creek THF	Red oak, White oak	51	X						X			X													X													
Urenholdt THF	White pine	52							X		X													X														
Wausaukee THF	White & Red pine, Aspen	47					X		X				X				X							X					X									
Champion Valley THF	Northern hardwoods	47								X			X							X									X									
Star Lake	Red pine	43					X						X							X								X						X				
Butler's Woods	Oak, Basswood, Maple	45	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X											X							
Nettleton	Northern hardwoods	38		X				X		X	X	X					X	X			X		X				X	X					X					X
Stone's Woods	Oak, Hickory, Maple	45	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X											X							
Shaugnessey's Woods	Oak, Hickory, Maple	45	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X											X							
NC-26	Balsam fir, Aspen	49					X	X				X		X				X		X		X	X	X	X		X											
NH-25	Northern hardwoods	51						X				X					X					X			X													
NH-138 (Argonne)	Northern hardwoods	56						X		X				X			X			X																		
NH-138 (Medford)	Northern hardwoods	58				X			X				X					X																				
NC-18	White spruce	49						X	X								X										X											
NC-32	N. White cedar	46										X												X						X								
Owens-Illinois	Northern hardwoods Conifers	64					X					X																										
MINNESOTA																																						
NC-56 (Pike Bay)	White pine	54	X				X					X					X					X																
NC-57 (Pike Bay)	Jack pine	53				X	X					X				X						X																
NC-59 (Little Fork)	Black spruce	54													X							X																
NC-76 (Cutfoot)	Red pine	49				X	X				X	X			X		X			X		X			X		X											
NC-78 (Cutfoot)	Red pine	50					X					X							X			X			X			X										
NC-79 (Bena)	Red pine	49					X					X					X					X					X											
NC-83 (Marcell-Clubhouse)	Red pine	44								X					X		X				X				X													
NC-84 (Lake 13)	Red pine	44												X	X	X	X				X	X				X	X				X	X						
NC-96 (Pike Bay)	Aspen	56					X				X					X					X																	
NC-98 (Aurora)	Jack pine	68					X																															
NC-142 (Portage Lake)	Red pine	47									X				X					X						X				X								
NC-155 (Birch Lake)	Red pine	57					X					X					X				X																	
NC-163 (Mando)	Red pine	57				X					X					X					X																	

[1] *An "X" denotes that at least one plot on the property was measured at the number of years after the earliest measurement given by the column label. Only Butler's, Stone's, and Shaugnessey's Woods were measured in their entirety every year.*

(8) Dates (month and year) of each measurement.

The master format consists of a maximum of 512 word blocks of binary information. The block length is specified because of input/output buffer length on the Control Data Corporation's Cyber '74 computer. Each word can contain up to 14 integer values to code information. The master format and contents of each word are given in figure 2. An example output of a permanent growth plot record is shown in figure 3. Specific objectives of the master format were to (1) maximize efficiency in reading/writing and storing the master files, and (2) have information in a standardized format because five or six different persons may be getting information from the master at any one time.

RETRIEVAL OF INFORMATION FROM DATA BASE

Because the information is written in blocked binary form with 14-character words, one must use simple FORTRAN statements to extract the desired values from a word in a block. For example, to analyze mortality, the master file is read and the desired information extracted to establish an analysis-specific file. Most of the sort word contents are normally carried into the analysis-specific files. This information, together with other information, aids in tracing any problem observations and for organizing analyses by state, species, mode of stand origin, etc. The analyses then proceed species-by- species for the 26 species groups for which functions are developed.

```
 Word

   1         Number of words in record

   2         Sort word

             I1  Mode of stand origin
             I2  Treatment
             I1  Replication
             I3  Data source (property number)
             I5  Plot number
             I1  Record number (1, or 2, or 3, or 4 if more
                     than 500 words on preceding record
                     (except for record 1))

 3-7         Site index (up to 5 SI-species combinations)

             I2  SI
             I3  Species for SI
             I3  Stand origin (last 3 digits of origin year)

   8         Plot invariate parameters

             I2  Forest type
             I2  Plot size (as denominator of fraction, i.e.,
                     5=1/5 acre plot)
             I3  Number of trees on plot
             I2  Number of measurements = mea

   9         Soils information

10-9+mea     Plot variable parameters

             I4  Date of measurement (MMYY)
             I3  BA/acre at time of measurement

10+mea,      Tree invariate parameters
11+2mea,
12+3mea,
 ...
             I3  Tree number
             I3  Tree species
             I2  Tree species group

11+mea-
12+2mea      Tree variable parameters

             I1  Status
             I1  Condition
             I3  DBH to last tenth inch (F3.1)
             I1  Crown class
             I1  Crown ratio
             I1  Tree quality
             I2  Form factor
             I3  Height
```

Figure 2.— *Lake States FREP binary master record format.*

```
   92   1000100000011   61105918   62375942   0   0   0   10701604   0
              1059026            1064037            1069048             1076053
  110501 4009800000000 1011000000000 1011900000000 1012926000064
  237526 4006000000000 1007200000000 1008400000000 1009735000000
  310501 4012800000000 1014000000000 1014700000000 1016326000068
  410501 4009500000000 1010300000000 1011100000000 1012727000000
  510501 4011600000000 1012800000000 1013700000000 3000000000000
  610501 4009500000000 1010700000000 1011700000000 1012126000065
  737526 4005900000000 1006900000000 1007800000000 1009036000000
  837526 4006000000000 1007000000000 1008000000000 1009335000000
  909506             0 4005300000000 1006000000000 1006738000000
 1037526             0 4005200000000 1006300000000 1007126000049
 1109506             0 4005600000000 1006500000000 1007228000040
 1209506             0 4005700000000 1006900000000 1007928000000
 1310501             0             0 4006100000000 1006834000000
 1437526             0             0 4005900000000 1007536000000
 1537526             0             0 4005200000000 1005845000000
 1609506             0             0             0 4005458000000
```

Figure 3.— *Sample output listing of a single plot from the master file. Contents and meaning of each word are given in the master format in figure 2.*

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POTENTIAL DIAMETER GROWTH FUNCTIONS

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When seeking an unknown value of a numerical variable it is common practice to bracket the unknown by two values—one greater than the unknown and the other less. Mathematicians have used this practice for many years to find the solution of nonlinear algebraic equations. A simple example is the problem of finding the value of x that satisfies the equation $x^2 = y$, when $y = 142$.

The square root of a number can be estimated by guessing a number such that its square is greater than y and then guessing another with square less than y; e.g., $12^2 = 144$ and $11^2 = 121$. The desired value is then known to be between 12 and 11. By judicious guessing one quickly gets several correct digits in the value of x.

The idea of establishing an upper and a lower bound to the rate of a biological process is a very useful modeling device. In the case of the accretion processes it is reasonable to take zero as the numerical value of the lower bound. This paper is concerned with estimating the largest possible numerical values—the potential—for increase in diameter at breast height (d.b.h.) by all major forest species in the Lake States. Our concern is with both the potential diameter growth rates of individual trees and the diameter growth potential of all trees in a stand.

The concept of a growth potential has been used in mathematical modeling of biological processes for many years (Verhulst 1965, Lotka 1956, Volterra 1931, Gause 1969). The potential is given by r in the generalized differential equation of population growth: $\frac{dY}{dt} = r\,f(Y)$.
The term r refers to the rate of self-renewal of the population in question. Its effect dominates the right-hand side of the equation as long as resources are not limiting.

Foresters have only recently begun using the concept of potential in forest growth models. Arney (1974), Hegyi (1974), Ek and Monserud (1974) have used potential height growth as the upper limit of growth. Potential height growth is usually estimated by taking the first forward difference, with respect to age, of equations to predict height based on site index and age (see Lundgren and Dolid 1970). The use of breast height diameter growth to characterize a tree's potential is less common than the use of height (Newnham 1964, Chen 1976). A disadvantage of this approach is that there are no standard functions relating tree and environment variables to diameter growth, as there are to relate tree and environmental variables to tree height.

In theory, the following tree and environment variables affect the amount of lateral stem growth at breast height: (1) current d.b.h., (2) amount of foliage, (3) respiring surface area, (4) distance from breast height to center of live crown, and (5) abiotic flux as reflected by site index. The relation between each of these variables and diameter growth was extracted from the literature by Brand:[1]

(1) The closer the crown to breast height, the more stem growth (Duff and Nolan 1953).

(2) Less foliage is needed on a good site (Assmann 1970).

(3) Amount of foliage is greater on a good site (Long and Turner 1975).

(4) Respiring surface area is related allometrically to d.b.h. (Pienaar and Turnbull 1973).

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[1] *Brand, G. 1976. Personal communication, St. Paul, Minnesota.*

There are many ways of combining variables used to characterize each of these relations. Two broad categories are strictly additive association and strictly multiplicative association. Of course, one may have combined additive and multiplicative.

APPROACH

Our objective was to develop species-specific diameter growth equations that characterize the potential of Lake States tree species to increase in d.b.h. We have used a combined additive-multiplicative model that requires knowledge of the following variables: d.b.h., crown class, crown ratio, and site index (age 50 base). Crown ratio is the ratio of full live crown length to total tree height.

Data Base

Individual tree diameter measurements at two points in time were collected on dominant and codominant trees of 26 species in Michigan, Wisconsin and Minnesota. A total of 51,149 trees came from permanent growth plots or from forest survey plots in Wisconsin; of these, 36,726 were high-quality dominant and codominant trees usable for estimating potential growth.

All trees had crown class and crown ratio estimates at the last measurement. Plot site index was also estimated. The geographical distribution of plots, and the distribution in the age-site matrix is given in Christensen *et al.* (1979).

The diameter growth (ΔD) for each tree was determined over a period approximating 10 years. This was the dependent variable in a nonlinear regression analysis. The independent variables were initial diameter (D), final crown ratio (CR), and plot site index (SI). These data for all dominants and codominants were grouped by species, as shown in the tabulation above, by 1-inch diameter classes, by 10-foot site index classes, and by 10-percent crown ratio classes. If a cell contained just one tree, it was included in the most appropriate adjacent class. For each cell the means were computed for each variable, i.e., $\overline{\Delta D}$, $\overline{D}$, $\overline{SI}$, $\overline{CR}$, as well as the standard deviation of diameter growth, $s_{\Delta D}$.

Species	Number of trees
Jack pine	4,625
Red pine	11,663
White pine	845
White spruce	1,772
Balsam fir	1,277
Black spruce	1,006
Tamarack	165
Northern white-cedar	1,070
Hemlock	140
Black ash	240
Cottonwood Silver maple Red maple	937
Elm	898
Yellow birch	343
Basswood	1,092
Sugar maple	3,753
White ash	866
White oak	517
Select red oak	1,555
Other red oak	290
Hickory	349
Bigtooth aspen	261
Quaking aspen	2,124
Paper birch	748
Other hardwoods	190
Total number of trees	36,726

The mean diameter growth, $\overline{\Delta D}$, for each cell applies to dominants and codominants. Since it was our desire to estimate the potential of trees to increase in diameter at breast height, it was assumed that the diameter growth values were normally distributed around this mean (see fig. 1). The potential is, of course, greater than the average. We took the potential to be the mean diameter growth plus 1.65 standard deviations ($\Delta D+1.65s_{\Delta D}$). This diameter growth corresponds to the 95th percentile of dominant and codominant diameter growth.

Mathematical Model

The following four mathematical models were examined. All were nonlinear in form and combined additive-multiplicative with a core Richards-type function that has anabolic and catabolic terms (Richards 1959):

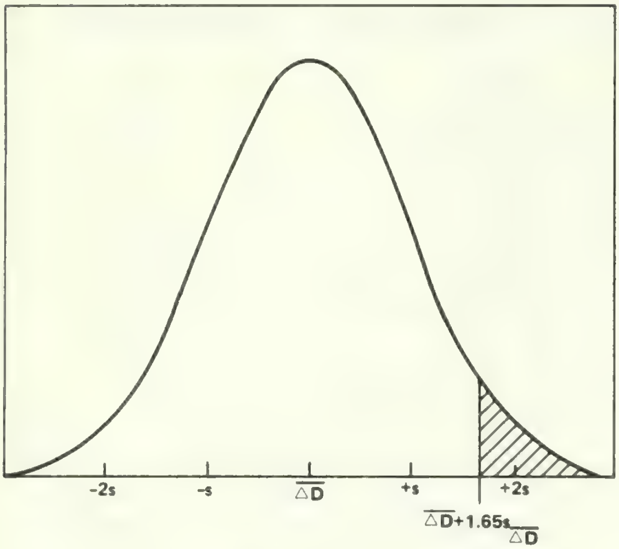

Figure 1.—*The assumed normal distribution of diameter growth of dominant and codominant trees for a 10-foot site index class and 10-percent crown ratio class. The shaded area represents the fastest-growing 5 percent of the trees.*

$$\frac{\Delta D}{\Delta t} = b_1 SI + b_2 D^{b_3} + b_4 CR\ D \qquad (1)$$

$$\frac{\Delta D}{\Delta t} = b_1 CR + b_2 D^{b_3} + b_4 SI\ D \qquad (2)$$

$$\frac{\Delta D}{\Delta t} = b_1 + b_2 D^{b_3} + b_4 SI\ CR\ D \qquad (3)$$

$$\frac{\Delta D}{\Delta t} = b_1 + b_2 D^{b_3} + b_4 SI\ CR\ D^{b_5} \qquad (4)$$

The pattern of each is $\frac{\Delta D}{\Delta t}$ = ["intercept" term] + [catabolic term] + [anabolic term]. The signs on b_1, b_3, b_4, and b_5 are positive, and b_2 is negative. The "intercept" term gives the growth approached as d.b.h. approaches zero; in equations (3) and (4)

$$\lim_{D \to 0} \frac{\Delta D}{\Delta t} = b_1.$$

This limit is a function of SI in (1) and of CR in (2). The catabolic term, $b_2 D^{b_3}$, has the form of an allometric relation, as required of a relation characterizing respiring surface area (Pienaar and Turnbull 1973). Several anabolic terms were tested. The terms in equations (3) and (4) make the most sense, because total tree height is multiplied by crown ratio, giving crown length. Stem diameter has often been related to crown diameter. The product of crown length and width gives an approximation, uncorrected for crown shape, of crown volume.

Fitting Procedures

Each of the above models was fit to both mean and potential ΔD values for each cell of each species using Marquardt's algorithm modified for weighted nonlinear least squares regression (Marquardt 1963). Model evaluation criteria were: qualitative behavior of the solution to each equation using the estimated parameters b_i; pattern formed by residuals (predicted minus observed diameter growth) plotted against initial diameter, crown ratio, and site index; and goodness of fit as measured by R^2. For some species the qualitative behavior of the solution was unrealistic because an insufficient number of observations was available at large diameters. To compensate, the silviculture literature was consulted and from it we determined the upper limit of d.b.h. for the species. A very small ΔD value was assigned to the diameter, an average crown ratio and site index were attached, and the "add" values were inserted into the data base as needed to insure more realistic behavior of the function at large diameters.

Results

Models (3) and (4) gave better results than (1) or (2) as judged by model selection criteria. The results of the regression analyses of models (3) and (4) for 26 species for both average growth and potential growth were examined and one or the other was selected as the best model. The coefficients, number of cells, and R^2 values are given in the tabulation. When the b_5 parameter is exactly 1.0, the model selected was number (3). Otherwise, model (4) was selected. Figure 2 shows potential diameter growth values for species commonly found in the pine type: red pine, white pine, jack pine, and quaking aspen. The crown ratio was set at 4.0 and site index at 65.

DISCUSSION

To use the potential diameter growth function it is necessary to know the initial diameter, crown ratio, and site index. Crown ratio is not a commonly collected tree variable, but the average crown ratio for a stand can be estimated by knowing mean stand basal area, mean diameter, and stand age (Holdaway *et al.* 1979).

The inferential population for equations (3) and (4), with coefficients in table 1, is the natural stands and plantations of the 26 species in Michigan, Minnesota, and Wisconsin. No attempt was made to separate trees in plantations from those in natural stands, because the individual tree is not thought to behave differently.

The approach used for potential diameter growth is somewhat analogous to that used for models based on potential height growth. The latter use height-age relations for dominants (site index curves). We used diameter growth-diameter relations for the fastest-growing dominants and codominants. By taking the 95th percentile of diameter growth, we intended to approximate diameter growth rates of forest trees not subject to significant competition from neighboring trees. We judged open-grown trees as not suitable for potential diameter growth studies because of the significant difference in the distribution of increment among bole, branches, and limbs.

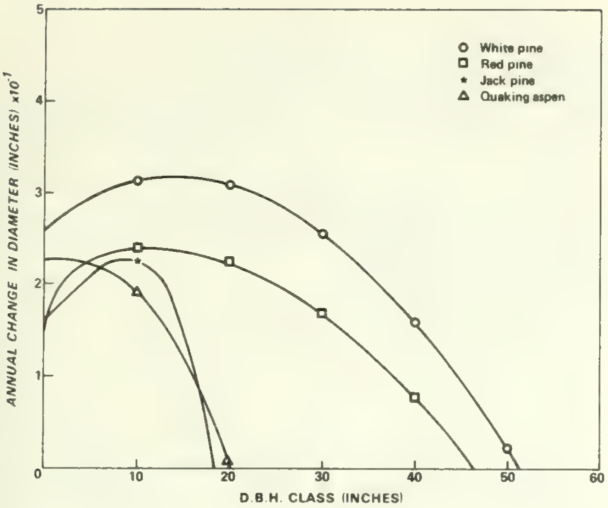

Figure 2.—*Predicted potential diameter growth values for species commonly found in the pine type in the Lake States. Site index is 65 and crown ratio is 4.0 for each species.*

Table 1.—*Number of cells and coefficients for average and potential diameter growth functions for 26 species in the Lake States*[1]

	Number of	Average						Potential					
Species group	groups	b_1	b_2	b_3	b_4	b_5	R^2	b_1	b_2	b_3	b_4	b_5	R^2
1 Jack pine	126	0.09349	−0.00005	2.9144	0.00003	1.0	0.44	0.16062	−0.000009	3.6245	0.00004	1.0	0.35
2 Red pine	282	.05309	−.00013	2.0468	.000197	.38337	.64	.09446	−0.00012	2.0596	.00035	.24225	.54
3 White pine	161	.15242	−.00030	1.9660	.00003	1.0	.34	.25578	−.00088	1.7263	.00004	1.0	.28
4 White spruce	72	.18789	−.00776	1.3904	.00006	1.0	.51	.17056	−.014516	1.0660	.00052	.27298	.74
5 Balsam fir	121	.037102	−.00026	1.9768	.00016	.37750	.64	.12200	−.00080	1.9890	.00006	1.0	.50
6 Black spruce	105	.06667	−.00049	2.1592	.00003	.95715	.26	.10713	−.00107	2.0017	.00006	.91127	.39
7 Tamarack	56	.05279	−.000002	3.4307	.00003	1.0	.29	.11147	−.00001	3.0685	.00003	1.0	.22
8 N white-cedar	93	.06480	−.00000002	4.7466	.00012	.15411	.41	.13403	−.000001	3.6880	.00002	1.0	.17
9 Hemlock	59	.11278	−.000000009	4.3699	.000007	1.0	.25	.16872	−.0000003	3.5738	.00001	1.0	.25
11 Black ash	84	.035027	−.000000001	5.3434	.00010	.46385	.41	.058807	−.000000006	5.0559	.00024	.31553	.25
12 Cottonwood													
13 Silver maple	176	.06793	−.00038	1.5944	.00020	.29971	.44	.10948	−.00004	2.2226	.00050	.06626	.30
14 Red maple													
15 Elm	179	.14862	−.00016	1.9910	.00002	1.0	.12	.28496	−.00182	1.5297	.00003	1.0	.06
16 Yellow birch	96	.11333	−.00005	2.3334	.000006	1.0112	.12	.15155	−.000003	3.3104	.00007	.57302	.18
17 Basswood	169	.16782	−.00025	1.8136	.000008	1.0	.16	.25402	−.000004	2.9396	.00001	1.0	.09
18 Sugar maple	272	.13309	−.00051	1.7002	.00002	1.0	.29	.18772	−.000007	2.5839	.00028	.08385	.33
19 White ash	139	.10829	−.00025	2.0926	.00003	1.0000	.36	.21167	−.000003	3.3131	.00001	.12430	.27
20 White oak	152	.08114	−.0000004	3.1795	.00004	.51666	.26	.12654	−.000004	2.7538	.00005	.62086	.21
21 Select red oak	286	.098793	−.0000002	3.3873	.00008	.41156	.38	.15535	−.00000010	3.5367	.00018	.25900	.22
22 Other red oak	92	.10142	−.0000002	3.7728	.00012	.20604	.46	.17358	−.00007	2.4451	.00003	.95222	.30
23 Hickory	93	.071908	−.000008	2.7884	.00003	.69376	.44	.16471	−.02161	1.3949	.00004	.71628	.26
24 Bigtooth aspen	79	.14120	−.00029	2.1217	.00003	1.0	.28	.23490	−.00942	1.1041	.00036	.15386	.33
25 Quaking aspen	201	.11789	−.00015	2.3618	.000042	1.0	.39	.21645	−.000091	2.6030	.000044	1.0	.31
26 Paper birch	112	.07565	−.00059	2.0175	.00005	1.0003	.48	.10971	−.00032	2.0236	.00034	.21288	.41
30 Other hardwoods	79	.19662	−.00954	1.0500	.00002	1.0	.44	.37510	−.02479	9.6288	.00004	1.0	.36
Total	3,284												

[1] Crown ratio variable used is 3.0 rather than 0.3. General model is $\frac{\Delta D}{\Delta t} = b_1 + b_2 D^{b_3} + b_4 SI\ CR\ D^{b_5}$.

To estimate stand potential growth, the mean stand d.b.h., mean crown ratio (either observed or predicted), and site index are substituted into equation 4, along with the appropriate coefficients from table 1; the potential growth of a single tree is then computed. This is the estimated rate of growth of a free-to-grow tree. Potential stand growth is simply the number of trees in the stand times the free-to-grow rate.

CONCLUSION

Potential and average diameter growth rates for 26 species in the Lake States are adequately predicted by combining initial tree diameter, crown ratio, and site index, into a nonlinear model containing three terms: intercept, catabolic, and anabolic. The intercept term is a species-specific constant, the catabolic is an allometric relation of tree diameter, and the anabolic term is a product of crown length and an allometric relation of tree diameter. Since the potential diameter growth function characterizes free-to-grow conditions, potential stand diameter growth is simply the product of tree potential and number of trees.

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ESTIMATING MEAN STAND CROWN RATIO FROM STAND VARIABLES

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The amount of foliage in a stand of trees is an important indicator of the growth one may expect from the stand. Although this relation has been known for decades, the amount of foliage is not an easily determined variable that can be used in equations to predict stand growth. Field measurements on permanent growth plots have traditionally concentrated on stem dimensions (i.e., diameter and height), with supplemental correlation studies to associate crown diameter with stem diameter and other stand variables. An exception is the national forest survey, which has included measurements on tree crown ratio for many years. Recall that crown ratio is the fraction of total tree height in full live crown. Throughout this paper we express the "fraction" as an integer between 0 and 10 — i.e., a crown ratio of 2 means a tree has 11-20 percent of total height in full live crown.

Crown ratio was found to be an important variable for predicting tree growth (Hahn and Leary 1979), and was incorporated into an equation to predict potential diameter growth in a stand. Because the potential growth equations require mean stand crown ratio as an independent variable, and some prospective users of the generalized growth projection system (Hahn and Brand 1979) may not have included this variable in their plot data, it is necessary to develop equations to approximate mean stand crown ratio.

MODEL RATIONALE

From a theoretical analysis it is suggested that the mathematical model should exhibit the following qualitative properties:

(1) solving the mathematical equation must give a value between 0 and 10,

(2) crown ratio must not increase as BA (basal area per acre) increases,

(3) crown ratio must ultimately decrease as age or average diameter increases, and

(4) the rate of change of crown ratio with basal area must decrease as age or average diameter increases.

The exact relations, rate coefficients, etc. appear to be species-specific.

The core model tried initially was:

$$\overline{CR} = \frac{b_1}{1 + b_2\ BA} \qquad (1)$$

Although this model satisfied condition (2) above, it did not satisfy (1) and, because only basal area is used, it did not satisfy the important conditions in (3) and (4). The additional variables of age and average diameter were used with equation (1) to produce models satisfying conditions (1) through (4).

METHODS

The initial data base (Christensen *et al.* 1979) consisted of 1,529 permanent growth plots in the Lake States. Based on methods of treating plots of mixed species (Leary and Holdaway 1979), each plot was assigned as a pure species plot or as a combination of up to three species. In this study only plots fitted as "pure" or as containing two species were used. The individual tree crown ratios, measured on each plot in the last measurement year, were averaged to obtain a species mean crown ratio ($\overline{CR}$). Plot basal area was averaged over the 10 years preceding the crown ratio measurement. When no measurement had been taken

10 years preceding, the measurement nearest to 10 years was used. Only plots with no major disturbances (i.e., losses to mortality and/or cutting) during the interval were included. If the final basal area was less than 90 percent of the initial basal area, a major disturbance was assumed to have occurred and the plot was not used. For all acceptable plots mean stand diameter (AD) was calculated at the final measurement year and the stand age (AGE) was calculated at the midpoint of the interval.

RESULTS OF ANALYSIS

Because of insufficient or poorly distributed data for some species, it was necessary to group species as follows:

Group number	*Species group*
1	jack pine
2	red pine
3	white pine
4	white spruce, balsam fir
5	black spruce, tamarack
6	northern white-cedar, hemlock
7	cottonwood, silver maple, red maple
8	black ash, white ash, elm, basswood
9	yellow birch
10	sugar maple
11	white oaks, select red oaks, other red oaks, hickory
12	bigtooth aspen, quaking aspen, paper birch

The analysis showed two patterns of relations — one for conifers and another for hardwoods. The conifers tended to have much larger crown ratios for low basal areas than did the hardwoods. Mean plot crown ratios for conifers were seldom greater than 8 or less than 2. The range for hardwoods was much smaller; crown ratios seldom exceeded 5 even at very low basal areas. Fourteen different models, each containing the core relation, were fit to the data from 12 species groups using nonlinear regression methods (Marquardt 1963). The following model was selected for conifers:

$$\overline{CR} = \frac{8e^{b_1 \text{AGE}} + 2}{1 + \frac{b_2}{\text{AD}} \text{BA}}, \text{ where} \qquad (2)$$

AD=arithmetic mean d.b.h.,

BA=basal area in square feet,

AGE=years from stand establishment, and

b_1, b_2=unknown numerical constants.

Equation (2) coefficients for each conifer species group are as follows:

Species group	b_1	b_2	R^2	*Standard error of estimate*	*Number of plots*
Jack pine	−0.0187	0.0849	0.38	3.5	123
Red pine	−.01270	.0504	.42	4.3	384
White pine	−.0060	.1399	.42	2.1	62
White spruce-balsam fir	−.0058	.0815	.71	3.7	52
Black spruce-tamarack	−.0039	.1045	.12	7.0	41
Northern white-cedar-hemlock	−.0213	.0055	.41	3.7	42

The amount and rate of change of crown ratio with age, average diameter, and basal area for hardwoods was quite different from that for conifers. In general, hardwood crown ratio changed very little over the range of stocking, size, and age available in the data base. The model for hardwoods was established as the following variation of the core model:

$$\overline{CR} = b_1 \text{AGE} + \frac{b_2}{1 + \frac{b_3}{\text{AD}} \text{BA}}. \qquad (3)$$

Coefficients in equation (3) for the hardwood species groups are:

Species group	b_1	b_2	b_3	R^2	*Standard error of estimate*	*Number of plots*
Cottonwood, silver maple, red maple	−0.0186	6.910	0.0476	0.46	2.2	27
Black ash, elm, basswood, white ash	.0000	3.04	.0000	NA	1.4	64
Yellow birch	−.0222	6.019	.0264	.37	2.6	16
Sugar maple	−.0064	4.707	.0282	.26	1.9	143
White oaks,select red oaks, other red oaks, hickory	−.0080	4.728	.0381	.32	1.2	112
Bigtooth aspen, quaking aspen, paper birch	−.0070	4.298	.0230	.28	2.3	112

The crown ratio values for the 64 plots of black ash, elm, basswood and white ash showed so little variation that the mean value was assigned to the coefficient b_2 (equation 3), and b_1 and b_3 were set at zero. Comparing equations (2) and (3) we see that coefficients b_2 (equation 2) and b_3 (equation 3) operate to achieve the same effect: reducing the mean crown ratio as basal area increases. The average rate of change for conifers is twice that for hardwoods. Another major difference between species groups is based on the "intercept" values — i.e., the crown ratio as basal area, age, and average diameter approach zero. For conifers, the "intercept" is 10, a full live crown. For hardwoods the intercept is b_2, and ranges from 6.9 for cottonwood, red maple, and silver maple to 3.04 for black ash, elm, basswood, and white ash. Mean stand crown ratios over a range of average diameters, basal areas, and ages are shown for red pine and sugar maple in figures 1 and 2.

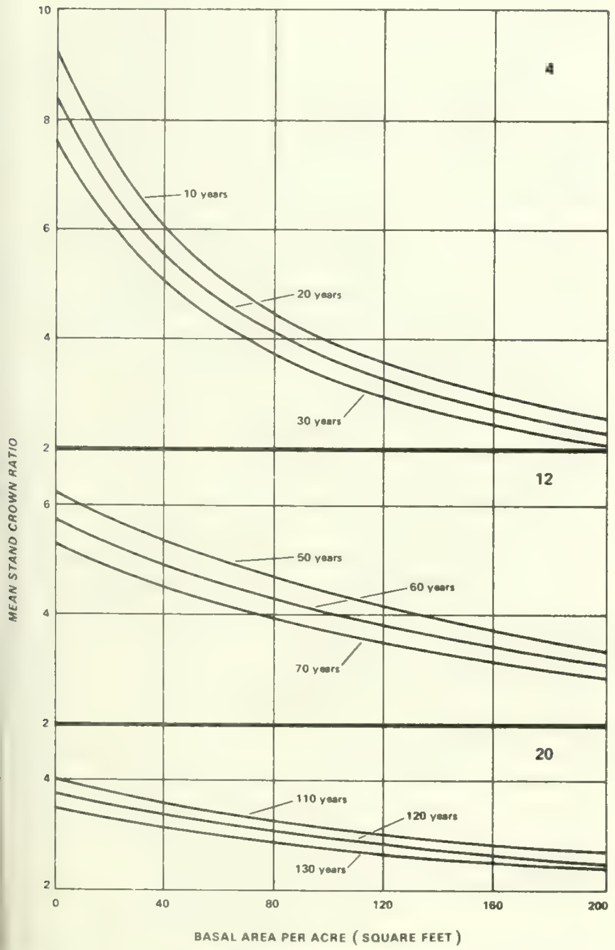

Figure 1.—*Mean stand crown ratio for red pine stands of selected ages and average diameters of 4, 12, and 20 inches.*

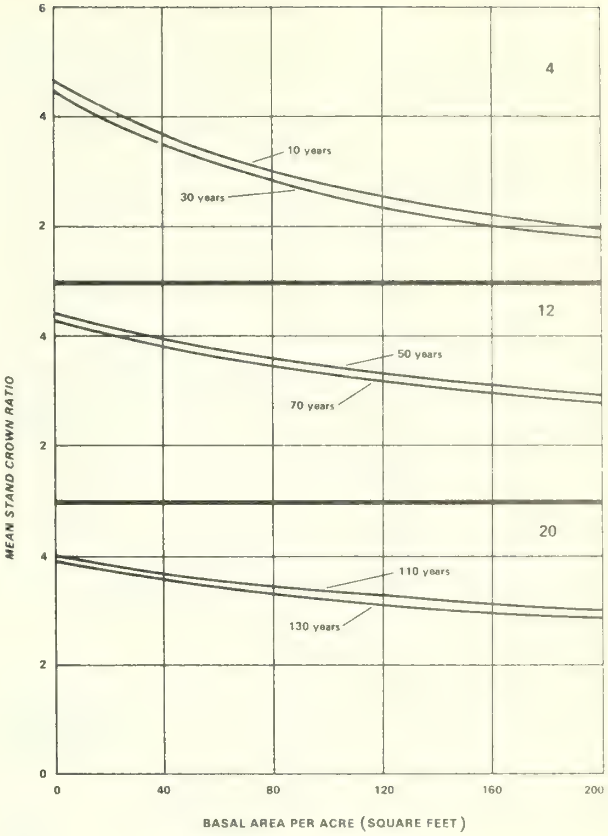

Figure 2.—*Mean stand crown ratio for sugar maple stands of selected ages and mean diameters of 4, 12, and 20 inches.*

DISCUSSION

Adequate estimates of mean crown ratio for a stand can be made if one knows the approximate mean basal area per acre over the last 10 years, the mean stand diameter, and the stand age. Better estimates can be made if one knows, say, the running average 10-year basal area. Simple point estimates of stand basal area will produce poor crown ratio estimates if one knows nothing about prior stand disturbances. A stand disturbance is less of a problem if the stand is old or the trees large. For example, if a red pine stand with an average d.b.h. of 6 inches, age of 40 years, and basal area of 150 square feet is cut back to 100 square feet with no change in average stand diameter, the predicted mean crown ratio would increase from 0.30 to 0.37. However, if the mean diameter had been 28 inches, the age 200, and the basal area 150 square feet, cutting back to 100 square feet with no change in average stand diameter would have had no significant effect on the mean crown ratio. When applied in the projection program (Hahn and Brand 1979), the running average basal area for the past 10 years is used instead of an average of only two or three values.

If cutting or mortality changes average stand diameter as well as stand basal area, the following relation holds for the models: a decrease in diameter as well as basal area (e.g., thinning from above) results in a lower crown ratio, whereas an increase in diameter and a decrease in basal area (e.g., thinning from below) results in a higher crown ratio. This relation is logical since larger trees of the same species in a stand (dominanats and codominants) tend to have higher crown ratios than smaller trees (intermediates and suppressed).

A generalized relation between mean crown ratio, age, mean d.b.h., and basal area, applicable to both conifers and hardwoods, is given in equation (4):

$$\overline{CR} = b_1\,AGE + \frac{b_2 e^{b_3\,AGE} + b_4}{1 + \frac{b_5}{AD}\,BA}. \qquad (4)$$

For conifers, b_1 is set at zero; for hardwoods b_2 is set at zero.

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MODIFIER FUNCTION

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A basic premise in the design logic for this generalized forest growth projection system is that the growth of an aggregate can be represented by a multiplicative combination of a potential growth nd a modifier of the potential. The modifier takes he form of a mathematical function since another premise is that the amount the potential is modiied depends on the amount of standing crop present. The purposes of this paper are to describe procedures and results of studies to determine how groups of trees interact within and between species.

The place the modifier function has in the basic projection system is shown in equation (1):

$$\frac{\Delta Y}{\Delta t} = \begin{bmatrix}\text{Potential}\\ \text{diameter}\\ \text{growth}\end{bmatrix} \begin{bmatrix}\text{Number}\\ \text{of}\\ \text{trees}\end{bmatrix} [\text{Modifier}]. \qquad (1)$$

At this stage in the analysis we assume that the potential diameter growth function is known, eaving the modifier function as the only function with unknown numerical constants. The relationhip of the modifier function to the data base and ther subsystems is shown in figure 1. Because the otential function is assumed known, estimation f the modifier cannot begin until it has been comleted. Also, shown connected to the potential unction is the crown ratio function. Under ideal ircumstances there would be no need for a crown atio function in the calibration phase because rown ratio would have been observed at all meaurements, hence actual observations could be used. In this study crown ratio was estimated only t the final measurement, in 1975 or 1976; thus, if he measurement interval selected for estimating he modifier was from a prior time, it was necesary to estimate the crown ratio used in the potential function. Because the modifier function coefficients depend on an estimated potential growth, which in turn may depend on an estimated crown ratio, the modifier function's sensitivity to variations in stand conditions may be less than it could be.

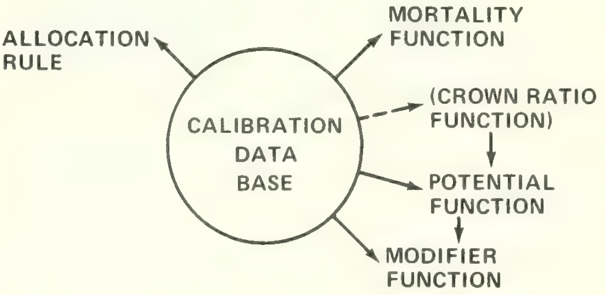

Figure 1. —*Relation of modifier function to data base, potential function, and crown ratio function. The latter is shown with parentheses and dashed line because when the crown ratio has been recently observed it is not necessary to use the crown ratio function in estimating numerical constants in the modifier function.*

REQUIREMENTS OF THE DATA BASE

Unlike the potential and mortality functions, the modifier function is based on information about all the trees on a plot. Thus, the data requirements relate to plot attributes rather than individual tree attributes. For a plot to be useful for estimating modifier function coefficients it must:

(1) have been measured three or more times,
(2) have been measured over approximately 10 years,
(3) exceed a minimum number of trees,
(4) exceed a minimum basal area density,

(5) be either a pure stand or a two-species mixture, and
(6) have not had excessive cutting or mortality in the measurement period.

The exact cutoff values for these six criteria are given in the methods section. Many plots were not used to estimate the modifier because they failed to meet one or more of the criteria.

METHODS USED TO SUMMARIZE, STORE, AND RETRIEVE DATA BASE INFORMATION

Before plot data are ready for analysis, the analyst must:

1. Take the data, as found in the data base, on the species present on each plot and transform them into a condensed form, recording the transformation.
2. Use this transformation information to consolidate all species present into a maximum of four species categories and then summarize the needed plot information into one physical record to enable the mass of data to be efficiently stored on disk files.
3. Design a system that enters a large file of information produced by step 2 (above) and picks out only those plots that match a specified species combination, "unpeels" the data, reorders the species if necessary, and lists the unpeeled data on a new file in a format ready for analysis.

Step 1 (above) needs to be discussed in more detail. We found in a preliminary study that the three needed measurements could be taken over as short an interval as 4 years without affecting the results. Whenever possible, however, we tried to have at least 6 to 8 years in the interval from first to third measurement. A computer program was written to locate where the cuts, mortality, and ingrowth occurred. From these results we manually selected an interval of at least 6 years with a minimum of disturbance due to death, cutting, or ingrowth, and a maximum number of live trees. In accommodating these constraints, the three-measurement interval tended to be as short as possible. This enabled us to use more than one interval from plots with five or more measurements. Using the chosen interval(s) we determined the percent basal area for each species on the plot, ordered the species by basal area, retained the first three species, and combined the remaining species into a miscellaneous category.

It was still necessary to reduce these species down to the principal ones. To accomplish this, a predominant species composition fitting rule was developed. The rule works approximately as follows for a plot with only two species: the plot is located in a coordinate system at the point (x_1,x_2), where x_i is the percent of plot basal area in species i (fig. 2). If the plot were a pure stand of species 1, the point would be located at coordinates (1,0); if it were a pure stand of species 2, it would be located at coordinates (0,1). All other mixtures would be located on a line between points (1,0) and (0,1) such that $x_1+x_2=1$. For a two-species plot, we calculate the distance from (x_1,x_2) to three points (1,0), (1/2,1/2), (0,1), and assign the plot to that species combination (pure species 1, two-species mixture, pure species 2) for which the distance is smallest.

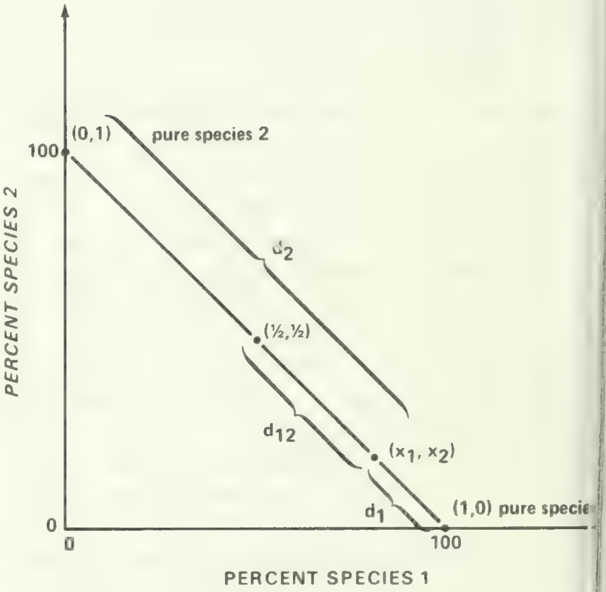

Figure 2. —*Schematic diagram of procedure for judging the composition of a plot containing two species. In this example d_1 is less than d_{12}, hence the plot will be considered a pure stand of species 1. Analogous methods are used in 3 and 4 dimensions for 3 and 4 species mixtures.*

In our work it was possible to have a maximum of four species categories. Since the species are put in descending order by percent basal area, the reference points for determining species fits are

(1,0,0,0)	corresponding to	pure species 1
(1/2,1/2,0,0)		two-species mixture
(1/3,1/3,1/3,0)		three-species mixture
(1/4,1/4,1/4,1/4)		four-species mixture

The distance from the point (x_1,x_2,x_3,x_4) to each of the four points was calculated and the species combination selected that had a minimum distance.

There was still a need to handle minor species dropped by the fitting rule. That is, something had to be done to species 4 if the fitting rule showed that the point (x_1,x_2,x_3,x_4) was closer to (1/3,1/3,1/3,0) than it was to (1/4,1/4,1/4,1/4). These species were added to a similar species based on a priority joining rule. Finally, for each plot we recorded the transformation that indicated the predominant species and what to do with all other species. For the purposes of this study only plots fit with one or two species were used and the others were skipped.

ANALYSIS METHODS AND RESULTS

Pure Stands

Once the plot information was summarized and stored in a retrievable manner, the pure stand analysis proceeded as follows: for a particular species, e.g., jack pine, the summarized data were used as boundary conditions in the nonlinear multipoint boundary value problem (Leary 1970, Leary and Skog 1972). Solve

$$\frac{\Delta Y}{\Delta t} = [\text{Potential diameter growth/tree}]\ [NT]\left[1-e^{-\beta/BA}\right] \quad (2)$$

subject to the boundary conditions

$Y(t_1) = k_1,\ Y(t_2) = k_2,\ Y(t_3) = k_3$, where

Y is the sum of tree diameters,

NT is the number of trees,

BA is the stand basal area $\left(BA = .005454\left(\frac{Y}{NT}\right)^2\right)$,

β is an unknown numerical constant (with units of basal area),

k_1,k_2,k_3 are the boundary conditions, and

$$\frac{\Delta Y}{\Delta t} = \frac{Y(t+1) - Y(t)}{(t+1) - t} \quad \text{(first forward difference).}$$

Other algebraic forms for the modifier were tested, this one most thoroughly

$$\frac{\alpha}{1 + \gamma\, BA}, \quad (3)$$

but were found to be less desirable based on their pattern of residuals.

Calculation of the potential diameter growth part of equation (1) requires use of mean stand crown ratio (Hahn and Leary 1979). Individual tree crown ratios on each plot had been recorded at the last measurement, but frequently the last measurement was not one of the times used to form the measurement set. Although most cases showed little difference between the β values resulting from observed or predicted crown ratios, we used only observed crown ratios whenever there was a sufficient number of interval sets. This practice resulted in a large reduction in the sets of measurements available for use. For example, red pine had 503 sets of measurements spanning three measurements, but only 241 included the last measurement and an observed crown ratio. Because we felt the observed crown ratio information was more precise, we used it unless doing so would have resulted in little or no information for a species.

The β values estimated for each measurement set judged to be pure were plotted against the mean stand diameter and their variation was studied. Based on these results, all measurement sets with 40 square feet or less of basal area stocking and with 50 percent (by number of trees) or more mortality and/or cutting between the beginning and final measurement were removed. Analysis showed the β values were independent of the number of trees, the site index, the interval length (5 to 29 years), and stand age to midpoint of the interval. There appeared to be a possible slight relationship between β and average summer temperature over the interval, but data were insufficient to warrant further study. The same held true for the effect of average summer rainfall on β.

Some species showed a location (Minnesota, Wisconsin, Michigan) effect, but the limited range of mean stand diameters for many species made its study inconclusive. Some investigations were made on various weighting approaches, but the only one that offered any benefit was to weight proportional to plot size.

Red pine, with 241 measurement sets, had the most data available to study any differences between natural stands and plantations. The plantations tended to have smaller average diameters with the same basic pattern as the natural sets except for a scattering of higher values at about 8 inches. A careful study was done to see if the cause of these higher values could be found, but it was unsuccessful. As a result, no separation as to mode of stand origin (plantation or natural) was made in the final analysis.

In determining a function to fit to the β's, we looked at those species with a fairly complete diameter range. Computing the average β for 2-inch average diameter classes indicated a nearly constant function that decreases somewhat at the lower diameter values. From this relation the function

$$\beta = b_1\,(1 - e^{\,b_2\,\overline{DBH}}) \qquad (4)$$

was chosen. A few representative graphs are given in figure 3.

Table 1 contains the coefficients b_1 and b_2 (equation 4) for various species and the number of three-measurement sets on which each is based. Only 490 measurement sets were usable after understocked plots, or those with high mortality or cut, were removed. Measurement sets were also lost because observed crown ratios were used, instead of predicted, whenever possible.

Mixed Stands

The mixed stand analysis proceeded similar to the pure stand analysis, but the model was expanded as follows:

solve

$$\frac{\Delta Y1}{\Delta t} = [PG_1]\,[NT_1]\left[1 - e^{\dfrac{-\beta_1 = f_1(AD_1)}{(BA_1 + \omega_1\,BA_2\,AD_2/AD_1)}}\right] \qquad (5)$$

$$\frac{\Delta Y2}{\Delta t} = [PG_2]\,[NT_2]\left[1 - e^{\dfrac{-\beta_2 = f_2(AD_2)}{(BA_2 + \omega_2\,BA_1\,AD_1/AD_2)}}\right]$$

with boundary conditions

$Y1(t_1) = k_{11}$ $Y1(t_2) = k_{12}$ $Y1(t_3) = k_{13}$

$Y2(t_1) = k_{21}$ $Y2(t_2) = k_{22}$ $Y2(t_3) = k_{23}$

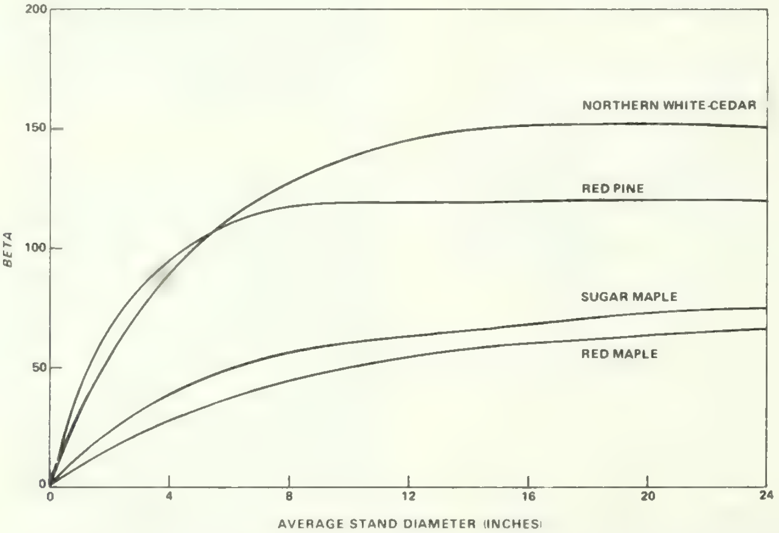

Figure 3. — *Sample monomeolecular functions relating β values to mean stand diameter. Conifer values tend to be considerably larger than hardwood values. The mathematical function is given in equation (4) and the numerical values are given in table 1.*

Table 1.—*Parameter values for equation (4)*[1]

Species	b_1	b_2	Sets of measurement intervals	Comments
Jack pine	112	−.4638	46	Predicted crown ratio used
Red pine	121	−.4462	241	Observed crown ratio used
White pine	117	−.1261	77	Predicted crown ratio used
White spruce	125	−.3652	11	Predicted crown ratio used
Balsam fir	86	−.4923	15	Predicted crown ratio used
Black spruce			9	data only for DBH 2″-4″ (use white spruce coefficients)
Tamarack			1	Limited data (use jack pine coefficients)
Northern white-cedar	155	−.2230	18	Observed crown ratio used
Hemlock			2	Limited data (use white pine coefficients)
Black ash			0	Assigned sugar maple coefficients
Cottonwood Silver maple Red maple	69	−.1434	7	Predicted crown ratio used
Elm			0	Assigned sugar maple coefficients
Yellow birch			1	Limited data (use coefficients for select red oaks)
Basswood			2	Limited data (use coefficients for select red oaks)
Sugar maple	74	−.1902	25	Observed crown ratio used
White ash			0	Assigned sugar maple coefficients
White oaks			4	Limited data (use coefficients for red oaks)
Select red oaks	73	−.1303	10	Observed crown ratio used
Other red oaks			0	Assigned coefficients of select red oaks
Hickory			0	Assigned coefficients of select red oaks
Bigtooth aspen			0	Assigned coefficients of quaking aspen
Quaking aspen	117	−.1366	21	Predicted crown ratio used
Paper birch			0	Assigned coefficients of quaking aspen
Total			490	

[1] For species in which the range of average diameters was small, or only a few observations were available, the estimated beta values were used as a guide in selecting a stubstitute beta function. When no data were available, the species was assigned the beta function parameters for a similar species; for example, we had no pure bigtooth aspen or paper birch plots, so they were assigned the beta function coefficients for quaking aspen.

where

$Y1, Y2$ are sums of diameters for species 1 and 2, respectively,

PG_1, PG_2 are potential diameter growth functions,

NT_1, NT_2 are numbers of trees,

AD_1, AD_2 are average diameters of trees in species 1 and 2,

f_1, f_2 are the monomolecular functions of average diameter (equation 4) for species 1 and 2,

BA_1, BA_2 are basal area $(.005454\ (Y_i / NT_i)^2)$ of species 1 and 2, and

ω_1, ω_2 are the unknown interaction terms that tell how species 2 affects species 1 and how species 1 affects species 2, respectively.

Only the plots judged to be two-species plots (figure 2) were used for this analysis.

We tested the ω values resulting from using both a potential function containing the observed crown ratio and the predicted crown ratio. The results were similar (actually slightly better for predicted crown ratio), as judged by the deviations of observations from predictions. Since there were more two-species plots available, we used the predicted crown ratio throughout the two-species analysis.

In the single species analysis we found that plots with less than 40 square feet of basal area had sharply decreased β values. The two-species analysis showed that between 30 and 40 square feet they were nearly the same as above 40 square feet. Thus, we used 30 square feet as the cutoff value for understocked plots instead of 40 square feet to avoid losing additional data. The cutoff criterion for mortality, cut, or ingrowth was 50 percent of initial or surviving trees. Very few plots had to be discarded because of these criteria.

From equation (5) it can be shown that if both ω_1 and ω_2 are exactly 1 and the ratio of average diameters is 1, we can say that species 2 affects species 1 as species 1 affects itself, and species 1 affects species 2 as species 2 affects itself. In this analysis, the following relationships between ω_1 and ω_2 were thought to be most reasonable and were examined:

$$\begin{array}{ll} [1] & \omega_2 \text{ and } \omega_1 \text{ estimated separately} \\ [2] & \omega_2 = 2 - \omega_1 \\ [3] & \omega_2 = 1/\omega_1 \\ [4] & \omega_2 = 2/\omega_1. \end{array} \qquad (6)$$

In relationship [1] there is no fixed relation between ω_1 and ω_2, in [2] the sum of ω_1 and ω_2 is equal to 2, in [3] the product of ω_1 and ω_2 is 1, and in [4] the product of ω_1 and ω_2 is 2.

Analysis of mixed plot data for each relationship in equation (6) showed that [1] is undesirable because ω_1 and ω_2 could vary widely with little difference in the goodness of fit of the solution of equation (5) to the observations. (This may have been caused by attempting to estimate four unknowns, ω_1 and ω_2 and initial conditions for Y1 and Y2, based on only six observations of the system state.) Relationship [2] between ω_1 and ω_2 gave very poor results as judged by residual pattern and residual magnitude. Relationships [3] and [4] both gave good results but $\omega_1 \omega_2 = 1$ was slightly better and more logical. Thus, for each two-species mixture we had the constraint that $\omega_1 \omega_2 = 1$. For each plot of, for example, jack pine-red pine, we had an estimated value of ω_1 and ω_2. The mean values for each two-species mixture is given in table 2 along with the number of plots. Because we are dealing with the product of two averages, $\bar{\omega}_1$ and $\bar{\omega}_2$, the product does not necessarily equal 1, but is usually near 1.

Table 2.—*Interaction terms* ω_1 and ω_2 for equation (5)

Species	ω_1	ω_2	Measurement sets available
Jack pine-red pine	2.757	0.483	4
Jack pine-quaking aspen	.829	1.355	3
Red pine-white pine	1.098	1.192	8
Red pine-quaking aspen	.455	2.261	2
White pine-white oaks	.776	1.432	2
White pine-select red oaks	3.500	.286	3
White pine-quaking aspen	1.783	.662	2
Balsam fir-quaking aspen	.581	2.327	16
Black spruce-northern white-cedar	.363	3.066	2
Hemlock-sugar maple	1.598	.977	5
Red maple-yellow birch	.859	1.205	2
Red maple-sugar maple	1.571	1.186	4
Red maple-select red oaks	2.321	.589	5
Red maple-paper birch	.389	2.677	2
Elm-basswood	.700	2.010	5
Elm-sugar maple	1.431	.824	11
Elm-white oaks	3.414	.293	2
Elm-select red oaks	2.090	.604	7
Elm-quaking aspen	.880	1.441	2
Basswood-sugar maple	.976	1.317	24
Sugar maple-white ash	1.589	.965	9
Sugar maple-select red oaks	2.357	.648	22
White ash-select red oaks	.427	2.346	2
White oaks-select red oaks	.977	1.601	10
White oaks-other red oaks	.282	3.546	2
Select red oaks-other red oaks	1.120	.893	3
Select red oaks-bigtooth aspen	.447	2.497	2
Select red oaks-quaking aspen	.499	2.324	2

DISCUSSION

The unit associated with β (equation 2) is square feet of basal area. Thus, the unit of b_1 in equation (4) is also square feet of basal area. The combination of equations (2) and (4) makes this clear

$$\left[1 - e^{\frac{-b_1 (1-e^{b_2 \overline{DBH}})}{BA}}\right] \qquad (7)$$

From this relation we interpret the β function to give the basal area at which a stand with mean diameter, $\overline{DBH}$, is growing at 63 percent of its potential. That is, when the exponent of e is -1, $1-\frac{1}{e}= 0.63$. On this basis, one would expect tolerant species to have higher function values than intolerant species. The softwoods in table 1 generally follow this pattern although one would expect jack pine to have a lower b_1 value than balsam fir. The hardwood estimates deviate more from the theoretical ordering. One would expect quaking aspen to have the lowest b_1 value. Instead, it has the highest.

Because of the way the model in equation 1 is assembled and the unknown numerical constants estimated, each subsequent step provides a check on previous steps. For example, the β value estimates provide a check on the potential function in the following ways: (1) if the β values are extremely large (recall the β unit is basal area) this means the potential function is predicting growth rates too low, and (2) if the β values exhibit a pattern that contradicts theory, such as quaking aspen having a higher b_1 value than sugar maple, then the potential function for one of the species may need more work. Likewise, when estimating ω_1 and ω_2, a check of the β functions for species 1 and 2, respectively, is made. For example, if two similar species have been observed growing together and the observations are used to estimate ω_1 and ω_2 in the relation

$$\omega_1 \, \omega_2 = 1,$$

one would expect ω_1 to be very close to 1. A value significantly different from 1 would indicate that one of the β functions is not adequately characterizing pure stand growth of the species.

Only pure stands and two-species mixtures were treated because the observational data simply will not support a thorough examination of three-species mixtures. Models for three- and four-species mixtures are built up from two-species models. For example, if we observe species 1 and 2 growing together and estimate ω_{12} and ω_{21} for their interaction, if we observe species 2 and 3 growing together and estimate ω_{23} and ω_{32} for their interaction, and likewise ω_{13} and ω_{31} for 1 and 3 growing together, then a three-species model is formed as follows:

$$\frac{\Delta Y1}{\Delta t} = [PG_1]\,[NT_1]\left[1 - e^{\frac{-\beta_1 = f_1(AD_1)}{(BA_1 + \omega_{12}\, BA_2\, AD_2\, /AD_1 + \omega_{13}\, BA_3\, AD_3\, /AD_1}}\right]$$

$$\frac{\Delta Y2}{\Delta t} = [PG_2]\,[NT_2]\left[1 - e^{\frac{-\beta_2 = f_2(AD_2)}{(BA_2 + \omega_{21}\, BA_1\, AD_1\, /AD_2 + \omega_{23}\, BA_3\, AD_3\, /AD_2}}\right] \qquad (8)$$

$$\frac{\Delta Y3}{\Delta t} = [PG_3]\,[NT_3]\left[1 - e^{\frac{-\beta_3 = f_3(AD_3)}{(BA_3 + \omega_{32}\, BA_2\, AD_2\, /AD_3 + \omega_{31}\, BA_1\, AD_1\, /AD_3}}\right]$$

The explicit assumption here, for example, is that species 2 affects species 3 the same whether or not species 1 is present.

For species mixtures where no information, or insufficient information, is available, a default value of 1 is given to the ω values, pending acquiring additional information.

CONCLUSION

When the potential growth of a plot or stand of trees of a single species is characterized by the product of a potential function, number of trees, and a modifier of the potential, the function

$$[1-e^{-\beta/BA}]$$

satisfactorily reduces the potential growth to that actually observed. The values of β are species-specific, being higher for conifers than for hardwoods, and higher for tolerant species than for intolerant species. For stands containing two-species mixtures, variation in the growth was satisfactorily estimated by using two equations:

$$\frac{\Delta Y1}{\Delta t} = [PG_1]\,[NT_1]\left[1-e^{\frac{-\beta_1=f_1(AD_1)}{(BA_1\,+\,\omega_1\,BA_2\,AD_2/AD_1)}}\right] \tag{9}$$

$$\frac{\Delta Y2}{\Delta t} = [PG_2]\,[NT_2]\left[1-e^{\frac{-\beta_2=f_2(AD_2)}{(BA_2\,+\,\omega_2\,BA_1\,AD_1/AD_2)}}\right]$$

We infer from this that mixtures of three or more species can be handled by expanding the number of equations.

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DIAMETER GROWTH ALLOCATION RULE

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THE PROBLEM

Forest growth models may be categorized in many ways. An often-used dichotomy is stand model vs. tree model. Munro (1974) presented a classification based on the use of inter-tree distances and primary input parameters (variables). In this paper we have added a third dimension to Munro's: projection variables. We feel this is important because one may choose not to project information at the level of detail potentially available, but at an aggregated level. For example, even though a tree list containing d.b.h., species, stem maps, etc. is available as input, one may choose to project the attributes of a class of trees. If, in going from the input form to the projection form, one aggregates tree attributes into class attributes, information is irretrievably lost unless a way can be found to disaggregate change in the projected variables.

There are advantages to maintaining and updating a tree list through time. It allows more useful output because individual trees can be aggregated according to a criterion of interest for output. This is especially important when the output criterion is not the criterion used to aggregate input to the projected variables. For example, output information is often desired according to various merchantability standards, such as 4.5-inch d.b.h. (pulpwood) or 11.0-inch d.b.h. (saw log). There is, however, ample evidence that these size criteria have no biological significance useful for projection purposes.

On the other hand, there are advantages to any approach that aggregates input information into a few classes for projection. Such approaches are more simple and economical, lending greater operational usefulness to the projection system.

The purpose of this paper is to present a simple rule for disaggregating change in a projected variable—i.e., of allocating change by a group of trees to the individual trees in the group. The following discussion assumes that the basic input information is in the form of a tree list containing tree species and d.b.h., and that this information has been aggregated into a single class for projection purposes.

APPROACH AND HYPOTHESIS

Two fundamentally different ways to approach the allocation (disaggregation) problem may be termed absolute and relative. An example will show the nature of their differences. Assume we have a 12-inch d.b.h. sugar maple on our tree list. It is one of a group of sugar maple trees whose collective attribute (e.g., the sum of their diameters) is projected for 10 years. From values of the collective attributes at the initial and final time we calculate change.

Implementing an absolute allocation rule to estimate the diameter growth on the tree would normally involve either consulting a table of mean diameter growth rates for sugar maple by size or size class, or solving a 10-year diameter growth equation for a 12-inch sugar maple tree. By applying the same procedure to all other trees on the tree list and summing the projected growths, the sum could be compared with the amount of change to be allocated. If, for example, the predicted sum exceeds the amount to be allocated, one could use a reduction constant for all trees.

Implementing a relative allocation rule would, on the other hand, consider the number of trees larger and smaller than the subject tree. According to these numbers, the subject tree is allocated an amount of diameter growth. Because the social environment of a tree is an important determinant of its growth, we have chosen the relative allocation rule.

The hypothesized relative allocation rule tested here is: growth of an individual tree in a stand is to the stand growth as growing stock of the individual tree is to the growing stock in the stand, or $\frac{\Delta d_1}{\Delta d_T} :: \frac{GS_1}{GS_T}$, where the known quantities are

Δd_T, GS_1, GS_T (stand change given by the projection equation, growing stock in the subject tree, growing stock total, respectively), and the unknown quantity is

Δd_1 (diameter change of the subject tree).

METHODS

Only calibration data base sample plots judged to be "pure" (Leary and Holdaway 1979) were used for this analysis. The trees on each sample plot were sorted in ascending order by d.b.h. and then grouped into 10 cells of nearly equal frequency, corresponding to the 1-10th percentile, the 11-20th percentile, etc., up to the 91-100th percentile. When the total number of trees, N, was not exactly divisible by 10, the extra trees were added, one per cell starting with the 1-10th percentile cell. Thus, each cell contained approximately 10 percent of the trees on a plot with the smallest 10 percent in the first cell and the largest 10 percent in the last cell.

The contents of each cell were analyzed for two attributes: (1) the growth of the trees in each cell relative to the total growth of all trees on the plot and (2) the growing stock represented by the trees in each cell relative to the total growing stock on the plot. Diameter growth per tree and sum of tree diameters were used as the respective variables.

Proportion of stand growth due the i^{th} cell was computed as follows:

$$\frac{\dfrac{\sum_{j=1}^{k_i} \Delta dbh_{ij}}{k_i}}{\sum_{i=1}^{10}\left[\dfrac{\sum_{j=1}^{k_i} \Delta dbh_{ij}}{k_i}\right]} = y_i \qquad (1)$$

where k_i is the number of trees in the ith cell, and Δdbh_{ij} is the periodic d.b.h. growth for the jth tree in the ith cell.

Proportion of growing stock in the ith cell was computed as follows:

$$\frac{\dfrac{\sum_{j=1}^{k_i} dbh_{ij}}{k_i}}{\sum_{i=1}^{10}\left[\dfrac{\sum_{j=1}^{k_i} dbh_{ij}}{k_i}\right]} = x_i \qquad (2)$$

where k_i is the number of trees in the ith cell, and dbh_{ij} is the diameter breast height of the jth tree in the ith cell.

These analyses gave two sets of 10 values for each plot having 10 or more trees:

x_i = the proportion of total growing stock in the ith 10-percentile cell, and
y_i = the proportion or total growth due to trees in the ith 10-percentile cell.

Proportion of growth and proportion of growing stock were computed for 10-percentile classes on each plot with 10 or more surviving trees in the time interval selected. Two intervals were selected on each plot: from the final measurement back approximately 10 years, and from the first measurement forward approximately 10 years. If overlap resulted, the plot was not used. A total of 1,599 plot observations were available for analysis. Each of the 1,599 observations consisted of two sets of 10 proportions: growth and growing stock, as well as additional plot descriptors (mean plot basal area at midpoint of the interval, mean stand diameter, site index, property and plot number).

Information on the 1,599 plots was sorted in order by species and mean stand basal area. Preliminary evaluations based on red pine plantation data showed a surprisingly linear relationship between proportion of growth and proportion of growing stock. The same linear relation was evident in the other plantation data available (jack pine and white spruce). Graphs of growth proportion against growing stock proportion for natural stands showed a marked difference from those for plantations. This was especially evident for plots with greater mean d.b.h. values and/or lower stand basal areas. Figures 1a and 1b show the differences in trends as plot basal area changes. Figure 1b is for red pine plantations and figure 1a is for red pine natural stands.

In both figures, there is a tendency for the relation to rotate around or near the point with coordinates .10,.10. This, of course, is to be expected since the plot data were divided into 10-percentile classes. As basal area stocking decreases the figures show three trends: the range in proportion of growing stock decrease, the range in proportion of growth decreases, and the slope of the relation changes from a very steep positive one at 179 square feet in figure 1a to slightly negative at 66 square feet in the same figure. Comparing these trends with those in figure 1b shows that the ranges also decrease, but the slope of the relation is still positive at 50 square feet.

Several approaches were used to develop mathematical equations to characterize the types of changing relationships between proportion of growth and proportion of growing stock. The attempt was basically to estimate parameters for a general equation fit to each set of observations based on basal area classes. For example, a four-parameter model fit to observations for each basal area class would yield one set of parameters (a,b,c,d):

$$GR_{prop} = f(GS_{prop}, a,b,c,d). \qquad (3)$$

Given a set of parameters (a,b,c,d) for each basal area class, the attempt was to develop an expression as follows:

$$a = f(BA), \text{ where}$$

a is a parameter in equation 3,
BA is mean stand basal area in square feet, and
f is an unknown function.

The general function, then, would be

$$GR_{prop}=f(GS_{prop},a=f_1(BA),b=f_2(BA), c=f_3(BA),d=f_4(BA)) \qquad (4)$$

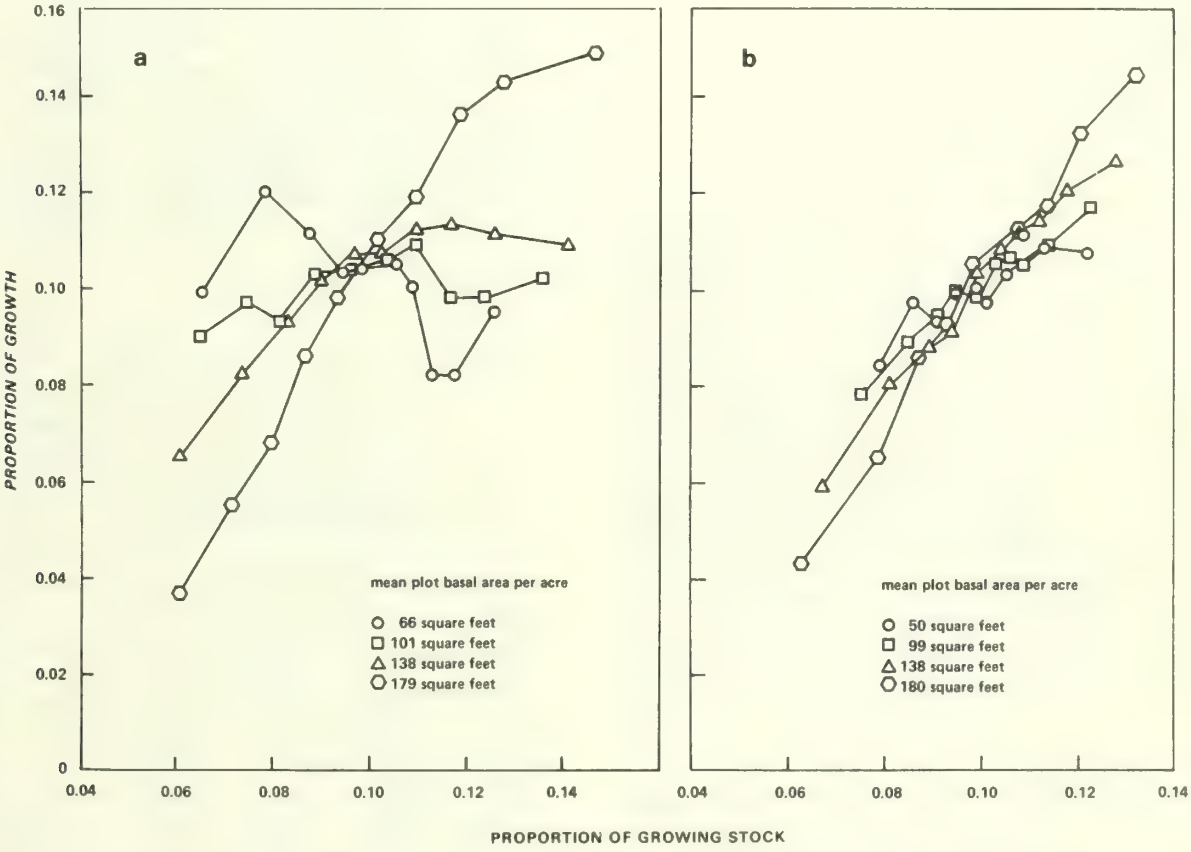

Figure 1.—*Proportion of growth compared with proportion of growing stock for (a) red pine natural stands and (b) plantations in the Lake States.*

where f_i ($i = 1,2,3,4$) are functions relating basal area (BA) to parameters a,b,c, and d.

This approach resulted in sets of parameter values—for example, a set of six b values that varied so widely that no relation between the b values and basal area could be established. As a result, this approach had to be discarded.

The approach finally used was to take the various graphic forms of relations between growth proportion and growing stock proportion shown in figure 1 and align a series of them on a light table so that they produced, as nearly as possible, a single smooth graph. To this single graph was added a new set of axes. The new coordinates of 17 points were read for segments of the composite graph and used as observations to estimate the parameters in an equation to characterize the composite graph. The function used was:

$$\log(GR_{prop}) = a_o + b(\log GS_{prop}) + c(\log GS_{prop})^2 + d(\log GS_{prop})^3 \quad (5)$$

where

log is logarithm to the base 10,

GR_{prop} is growth proportion,

GS_{prop} is growing stock proportion, and

a_o,b,c,d are unknown numerical constants.

Estimated values of the numerical constants are

$a_o = -2.379$

$b = -5.077$

$c = -3.972$

$d = -.2964$

($R^2 = 0.986$, Standard error $= 0.0204$). A graph of this function is shown in figure 2.

The strategy in putting together a composite relation is to have a mathematical function that possesses all the required types of shapes. The desired shape for a particular situation can be obtained simply by translating the axes so that the observed data coincide with a segment of the composite function graph. Because of the analogy with the giant tree concept (Grosenbaugh 1954), equation (6) is called the "giant function".

$$GR = k_1 + 10^{(a_o + b(\log(GS+k_2)) + c(\log(GS+k_2))^2 + d(\log(GS+k_2))^3)} \quad (6)$$

where a_o,b,c,d have the numerical values given above,

k_1 is the vertical translation of the axes, and

k_2 is the horizontal translation of the axes.

Observations of the growth proportions and growing stock proportions for basal area classes, such as shown in figure 1, were used to determine values of k_1 and k_2 for each basal area class for each species. Table 1 shows k_1 and k_2 values for eight red pine basal area classes for natural stands. The equation used to characterize the relation between k_1 and mean basal area is a simple parabola:

$$k_1 = a_1 + a_2BA + a_3BA^2 \quad (7)$$

where

a_1,a_2,a_3 are unknown numerical constants, and the function for k_2 is

$$k_2 = b_1(1 - e^{b_2(b_3 - BA)})^{b_4} \quad (8)$$

where

b_1,b_2,b_3 and b_4 are unknown numerical constants.

Constants a_i, $i = 1,2,3$ and b_i, $i = 1,...4$ were determined by linear and nonlinear regression methods, respectively, to give the following generalized form to the giant function:

$$GR = k_1 + 10^{(a_o + b(\log(GS+k_2)) + c(\log(GS+k_2))^2 + d(\log(GS+k_2))^3)} \quad (9)$$

where a_0,b,c,d are known constants for the giant function, and k_1 and k_2 are computed from plot basal area using equations (7) and (8).

In most cases it was necessary to examine the observations and assign numerical values to b_1 and b_3 in equation (8). Table 2 gives the coefficients of equations (7) and (8) for all species with sufficient data.

Table 1.—*Vertical (k_1) and horizontal (k_2) translation values for giant function to account for variation in relation between growth proportion and growing stock proportion for red pine natural stands (groups are by basal area classes)*

Basal area		k_1	k_2	R^2	No. of plots
Mean	Range				
65.6	(20-69)	-.1060	.1346	.42	8
79.5	(70-88)	-.1111	.1174	.44	21
101.5	(90-109)	-.1099	.0961	.53	52
119.1	(110-129)	-.1043	.0826	.93	151
137.9	(130-149)	-.1009	.0734	.97	86
156.0	(150-166)	-.0985	.0673	.96	39
178.9	(170-189)	-.0565	.0315	.99	19
197.6	(191-207)	-.0689	.0396	.71	5

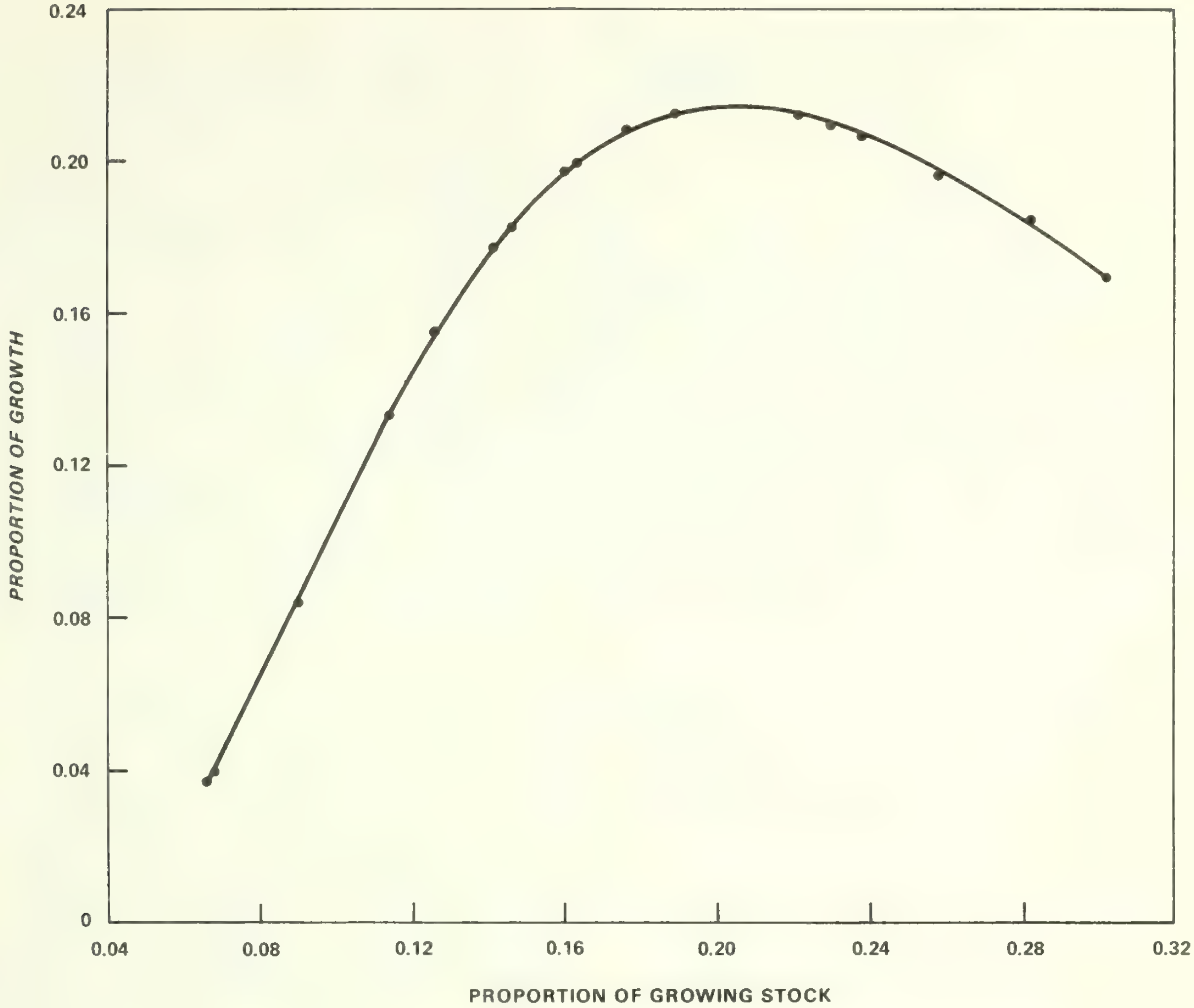

Figure 2.—*Graph of composite function in equation 5 showing location of 17 observations from separate graphs.*

RESULTS AND DISCUSSION

The functions to predict translation values, k_1 and k_2, show a considerable difference in the pattern of translations as basal area increases. Figure 3 shows the patterns for Lake States species with sufficient plots judged to be pure. Species differences relate primarily to the magnitude of k_1 and k_2, and the rate at which k_1 and k_2 approach zero. In general, tolerant species' values approach zero very slowly while intolerants rapidly approach zero. Quaking aspen appears to be an exception to this statement.

Small differences between species' k_1 and k_2 values can make a sizable difference in the relation between growth proportion and growing stock proportion. For example, the k_1 and k_2 values for red pine natural stands and plantations (figs. 3g and 3h, respectively) are very similar, yet the pattern for 3g produces the relations in figure 1a and that for 3h produces the relations in figure 1b.

The total sequence of operations in predicting growth proportion is given schematically in figure 4. Four input quantities are required for a given tree and stand to determine the tree's d.b.h. growth: total stand growth (from the stand component projection equation), d.b.h. of the *i*th tree, sum of tree diameters on the plot, and the total stand basal area.

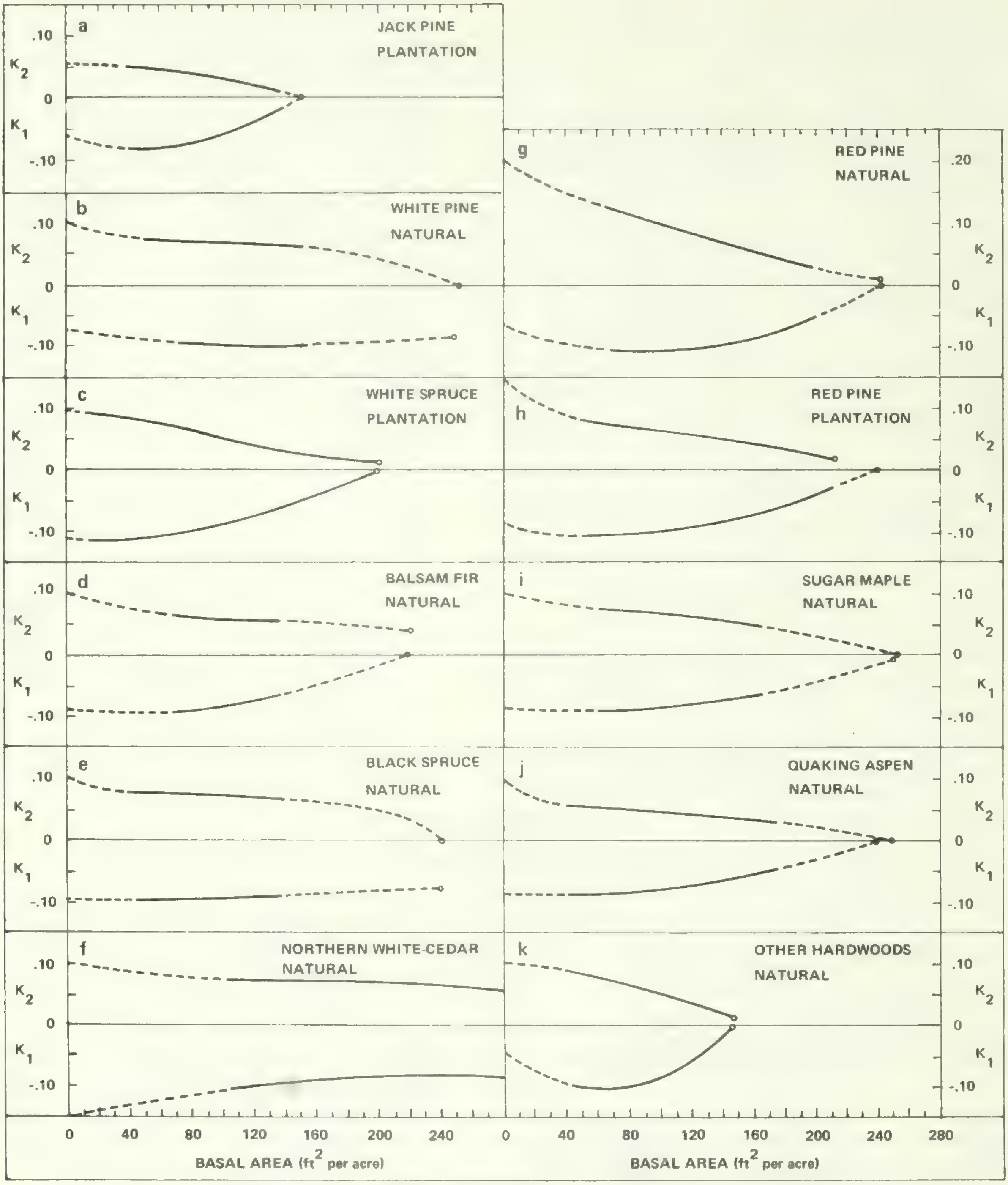

Figure 3.—*Translation values k_1 and k_2 for Lake States species. The solid lines denote the range of basal area for which data were available. The dotted lines are extrapolations based on equations (7) and (8) using coefficients in table 2.*

Table 2.—*Coefficients of equations (7) and (8) used to predict vertical and horizontal translations of axes so that appropriate section of giant function is used to characterize growth proportion–growing stock proportion*

	k_1 (vertical)			**k_2 (horizontal)**			
Species	**a_1**	**a_2**	**a_3**	**b_1**	**b_2**	**b_3**	**b_4**
Jack pine (plantation)	-.630 E-01	-.730 E-03	.770 E-05	.10 E 00	-.4000 E-02	.150 E+03	.7400 E 00
Red pine (plantation)	-.844 E-01	-.540 E-03	.380 E-05	.15 E 00	-.5585 E-02	.300 E+03	.2139 E+01
(natural)	-.643 E-01	-.968 E-03	.500 E-05	.20 E 00	-.9400 E-02	.300 E+03	.4102 E+01
White pine (natural)	-.736 E-01	-.350 E-03	.140 E-05	.10 E 00	-.7300 E-03	.250 E+03	.1759 E 00
White spruce (plantation)	-.111 E 00	-.100 E-03	.339 E-05	.10 E 00	-.1799 E-01	.250 E+03	.8264 E+01
Balsam fir (natural)	-.871 E-01	-.242 E-03	.283 E-05	.10 E 00	-.1720 E-02	.250 E+03	.3479 E 00
Black spruce (natural)	-.100 E 00	.620 E-04	.800 E-07	.10 E 00	-.3190 E-02	.250 E+03	.3724 E 00
No. white-cedar (natural)	-.154 E 00	.583 E-03	-.120 E-05	.10 E 00	-.2018 E-02	.400 E+03	.3724 E 00
Sugar maple (natural)	-.840 E-01	-.240 E-03	.240 E-05	.10 E 00	-.6200 E-02	.250 E+03	.8322 E 00
Quaking aspen (natural)	-.819 E-01	-.247 E-03	.248 E-05	.10 E 00	-.3470 E-02	.250 E+03	.7540 E 00
Other hardwoods (natural)[1]	-.394 E-01	-.196 E-02	.150 E-04	.10 E 00	-.2297 E-01	.200 E+03	.6384 E+01

[1] Red maple, elm, basswood, yellow birch, white oak, select red oak.

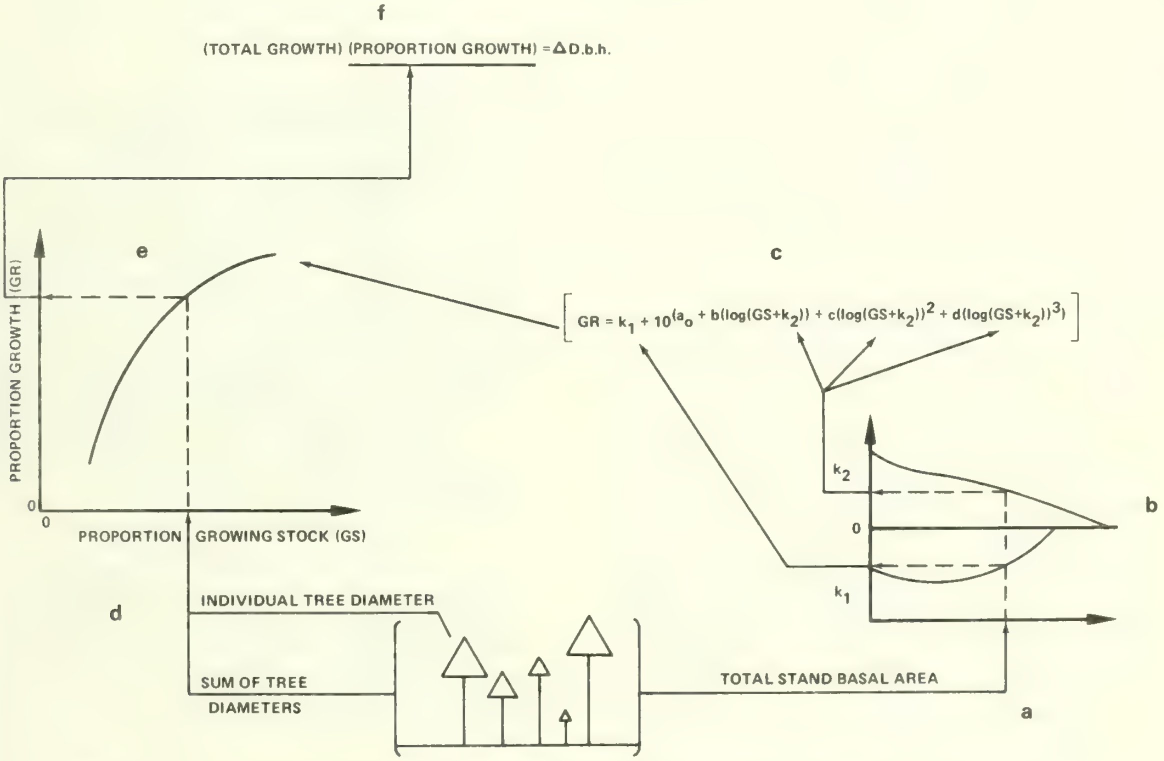
f
(TOTAL GROWTH) (PROPORTION GROWTH) = ΔD.b.h.
e
PROPORTION GROWTH (GR)
0
0
PROPORTION GROWING STOCK (GS)
c
$GR = k_1 + 10^{(a_0 + b(\log(GS+k_2)) + c(\log(GS+k_2))^2 + d(\log(GS+k_2))^3)}$
k_2
0
k_1
b
d
INDIVIDUAL TREE DIAMETER
SUM OF TREE DIAMETERS
TOTAL STAND BASAL AREA
a

Figure 4.—*Sequence of steps in the estimation of diameter growth for an individual tree in a stand. Steps a, b, and c establish the relation between growth proportion and growing stock proportion. Steps d, e, and f apply the relation to all trees in a stand. Total growth at step f comes from the projection equation.*

In the projection procedure each tree is treated individually rather than being grouped into 10-percentile classes. Considering a single tree on a plot of N trees is equivalent to dividing the plot into $\frac{1}{N}$ 100-percentile classes. In this case the relation between proportion of growth and proportion of growing stock should have the same shape as the 10-percentile graph but should be centered at $\frac{1}{N},\frac{1}{N}$ instead of (.10,.10). This can be accomplished by transforming the per-tree growing stock value to a 10-percentile class value. The latter value can be used as in figure 4, step e, and then be transformed from a 10-percentile growth proportion value to a $\left((\frac{1}{N})100\right)$ percentile growth proportion value. The conversion relations are based on the following proportions:

$$\frac{x_0}{X} :: \frac{\frac{1}{N}}{.10} \quad \text{or } X = x_0\,(.10)N$$

where

x_0 is the per tree growing stock proportion,
N is the number of trees, and
X is the 10-percentile growing stock proportion.

The value X is used as in figure 4e and a 10-percentile growth proportion is computed. This value is transformed back to a $\left((\frac{1}{N})100\right)$ percentile basis using the following relation:

$$\frac{y_0}{Y} = \frac{\frac{1}{N}}{.10}, \text{ or } y_0 = \frac{Y}{(.10)N}$$

where

y_0 is the per tree growth proportion,
N is the number of trees, and
Y is the 10-percentile growth proportion.

Because of the rather complicated procedures used to estimate all the giant function parameters, we used observed growing stock proportion and observed basal area, and computed a predicted growth proportion. These values were compared with the observed growth proportion. It appeared that no systematic bias had been introduced into our procedures because the deviations of predicted from observed were as a rule normally distributed about zero for both the percentile class and stand basal area. This test does not, of course, constitute an independent test; rather, it simply checks for bias introduced by our procedures.

CONCLUSION

The growth of an individual tree in a stand is a function of its position in the stand and of the stand growth. The initial hypothesis

$$\frac{\text{tree growth}}{\text{stand growth}} :: \frac{\text{tree growing stock}}{\text{stand growing stock}}$$

is overly simplistic. The growth proportion is related to growing stock proportion in a nonlinear manner that changes with basal area stocking levels. Furthermore, the nonlinear relation differs between natural and plantation stands of the same species.

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MORTALITY FUNCTIONS

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Knowing an individual tree's likelihood of dying within the next year is essential to a tree-model forest growth simulator. A mechanism for selecting trees to be removed from a stand as a consequence of mortality is an integral feature of the North Central Forest Experiment Station's generalized forest growth projection system (Leary 1979).

A tree's probability of dying depends upon its ability to cope with its environment. The tree itself, its neighboring trees, and numerous additional influences including light, moisture, nutrients, insects, and fungi combine to form the unique niche for the individual tree.

How might we assess the tree's response to the conditions of its neighborhood? One of the simplest indicators is the tree's vigor as reflected in its growth. Diameter growth rate is a readily obtainable, direct measure of the tree's ability to withstand the stresses of life.

Diameter growth rate is the key tree characteristic in the species-specific mortality functions presented in this paper. We attempted to select a common functional form for all species, with unique parameters for each species.

DATA ORIGIN

Permanent growth plot data were available for the major forest tree species in Minnesota, Wisconsin, and Michigan (Christensen *et al.* 1979). Most individual tree records contained measurements for at least three points in time, permitting calculation of an annual mortality rate for a given growth rate. Determining diameter growth rate required two diameter measurements; determining the tree's status (live or dead) and subsequently, the mortality rate, required a third measurement. The time between measurements ranged from 1 year to more than 10, with the most frequent interval being 5 years.

Intervals of at least 2 years but no more than 6 were chosen to establish a reliable measure of diameter growth rate. A comparable time interval (2 to 6 years) following growth rate determination was chosen for recording tree status.

These criteria reduced the size of the data base eligible for use in developing the mortality function. Even so, more than 47,000 trees (table 1) had the required three measurements. The tree count ranged from 18,208 for red pine and 7,350 for sugar maple down to about 100 for white spruce, tamarack, and bigtooth aspen.

Furthermore, many of the trees had more than three measurements that met the time requirements. However, only one set of measurement data—one diameter growth rate followed by a status observation—was used from each tree when deriving the mortality function. This set was chosen at random for each tree where two or more sets were available.

The number of trees by species in the final mortality data base is presented for each diameter growth rate class (table 1) and for each diameter class (table 2).

MORTALITY RATE

Individual trees either lived, (mortality zero), or died, (mortality 1.0). Diameter growth class mortality rates, however, depended upon the composite of the individual rates of those trees forming the class.

Growth class limits chosen were 0.0 inch (no growth), 0.02 inch, 0.04 inch, and so on up to 0.30

Table 1.—*Number of trees used in estimating mortality rates and parameters, by 5-year diameter growth classes*

	Five-year diameter growth class (inches)								
	.00-.09	.10-.19	.20-.29	.30-.49	.50-.69	.70-.89	.90-1.0	Over I.0	Total
Jack pine	104	165	178	492	833	763	718	528	3,781
Red pine	528	605	1,033	3,987	4,571	3,663	2,040	1,781	18,208
White pine	49	44	55	130	139	189	170	407	1,183
White spruce	3	2	6	10	12	25	9	39	106
Balsam fir	118	207	234	562	648	431	271	331	2,802
Black spruce	12	34	59	123	96	43	21	11	399
Tamarack	1	5	6	16	19	8	3	3	61
N. white-cedar	0	4	11	42	53	30	5	5	150
Hemlock	17	23	34	92	68	61	39	22	356
Black ash	8	10	21	45	42	23	10	5	164
Red maple	36	35	52	193	246	221	166	185	1,134
Elm	168	65	141	258	241	204	234	374	1,685
Yellow birch	38	32	51	143	129	100	51	53	597
Basswood	103	59	110	227	262	286	328	348	1,723
Sugar maple	402	216	538	1,145	1,447	1,347	1,214	1,041	7,350
White ash	20	22	60	129	131	182	237	319	1,100
White oak	33	29	50	117	103	66	30	18	446
Select red oaks	19	37	50	216	323	263	250	235	1,393
Other red oaks	11	4	21	28	32	20	13	11	140
Hickory	22	24	60	114	67	29	13	7	336
Bigtooth aspen	0	1	4	20	20	27	20	16	108
Quaking aspen	105	213	198	398	382	389	443	791	2,919
Paper birch	64	86	91	165	167	99	78	55	805
Other hardwoods	16	20	48	54	29	36	20	26	249
Noncommercial	101	22	70	77	24	10	3	2	309
Total									47,504

inch per year. These limits correspond to 5-year growth remeasurements (as mentioned earlier, 5-year remeasurements prevailed in the data base) of zero diameter growth, 0.1 inch, 0.2 inch, etc.

The mortality rate (R), the annual mortality for a growth class, was calculated from the more readily determined annual survival rate (SR), with R=1−SR.

If we assume the SR for a species to be the same each year of the 2- to 6-year status measurement interval, while allowing a tree to die but once with its demise being independent of others of the species, we have

$$\sum S_i = \sum N_i SR^i \,. \qquad (1)$$

In (1) i is the length of the status observation interval, S_i is the number of trees surviving the i^{th} interval, and N_i is the number of live trees at the beginning of the i^{th} interval.

These terms become more meaningful if we examine real status data, for example, the status of 528 "no growth" red pine trees:

Number of live trees (N_i) at second measurement	Number of years (i) to third measurement (status)	Number of live trees (S_i) at status measurement
0	2	0
16	3	13
31	4	29
417	5	347
64	6	44

Table 2.—*Number of trees used in estimating mortality rates and parameters, by d.b.h. class*

	D.b.h. in inches at second measurement (prior to status observation)																
Species	**to 1.5**	**1.6-2.5**	**2.6-3.5**	**3.6-4.5**	**4.6-5.5**	**5.6-6.5**	**6.6-7.5**	**7.6-8.5**	**8.6-9.5**	**9.6-10.5**	**10.6-11.5**	**11.6-12.5**	**12.6-13.5**	**13.6-14.5**	**14.6-15.5**	**15.6-16.5**	**16.6& larger**	**Total**
Jack pine	62	426	851	482	477	509	362	199	159	103	51	42	20	16	14	4	4	3,781
Red pine	12	91	234	928	1,937	2,889	2,851	2,221	1,811	1,491	1,124	853	628	432	320	183	203	18,208
White pine				23	72	64	70	70	76	75	81	81	78	82	79	71	261	1,183
White spruce	2	11	12	10	7	9	19	12	10	5	3	1	1	2	1		1	106
Balsam fir	92	596	631	463	298	303	207	107	61	22	12	5	4	1				2,802
Black spruce	3	12	35	44	68	132	80	16	6	3								399
Tamarack		3		1	9	20	11	10	3	2	2							61
N. white-cedar			1	1	3	36	34	21	27	15	6	4		1			1	150
Hemlock					30	36	44	33	35	30	33	24	23	26	16	12	14	356
Black ash				9	17	47	33	20	7	14	8	5	1	1	2			164
Red maple		7	3	19	97	237	185	156	115	92	74	50	22	28	15	10	24	1,134
Elm		18	69	119	156	178	180	175	172	155	136	85	65	46	35	33	63	1,685
Yellow birch		1		6	62	140	114	61	56	54	28	12	22	15	7	8	11	597
Basswood		20	33	68	148	225	220	195	191	170	134	72	54	33	32	27	101	1,723
Sugar maple	23	252	269	743	1,123	1,324	1,028	705	486	336	234	187	135	113	101	86	205	7,350
White ash		10	20	51	86	150	139	154	142	121	94	61	29	16	11	5	11	1,100
White oak		2			10	5	28	39	49	60	45	49	26	29	29	17	58	446
S. red oak				1	26	72	87	90	85	109	134	120	118	119	79	83	270	1,393
Other red oaks	3	7	10	13	12	6	6	3	6	12	17	9	6	9	6	3	12	140
Hickory		2	4	7	11	14	50	82	70	34	29	17	6	5	3		2	336
Bigtooth aspen					3	20	18	15	6	12	19	11	3	1				108
Quaking aspen		21	98	313	304	439	513	448	300	234	147	57	29	7	4	4	1	2,919
Paper birch		169	128	72	77	132	113	55	29	14	6	4	2	1	2		1	805
Other hardwoods		10	3	11	25	30	38	25	26	18	23	18	6	7	3		6	249
Noncommercial		28	39	51	85	49	30	15	7	5								309

If the status observation follows the second diameter measurement by 2 or more years and the status interval is of common length for all trees (i.e., one level of i), then (1) reduces to $S = N\,SR^{YR}$, where YR corresponds to the length, in years, of the observation interval. This yields $SR = (S/N)^{1/YR}$ and can be solved by substituting the observed N, S, and YR in the function. Based on the second line in the tabulation ($i = 3$), the annual survival rate, SR, is $(13/16)^{1/3}$ or 0.933. Calculating further, SR = 0.983 for $i = 4$, 0.964 for $i = 5$, and 0.939 for $i = 6$.

When several different status interval lengths are encountered, as with $i = 3, 4, 5$, and 6, application of equation (1) will yield a composite SR for all intervals. Substituting observed values in $\sum S_i = \sum N_i SR^i$ yields $433 = 16\,SR^3 + 31\,SR^4 + 417\,SR^5 + 64\,SR^6$. Solving, we find SR to be 0.9611 and R to be 0.0389.

We then have $\sum S_i = 433$ and $\sum N_i SR^i = 433.05$ with the red pine data, both a check on our calculations and the completion of the demonstration. In summary, we have:

N_i	i	S_i	$N_i SR^i$
0	2	0	0.00
16	3	13	14.20
31	4	29	26.45
417	5	347	341.96
64	6	44	50.44

Inspection of each species' mortality data revealed that decreasing mortality was associated with increasing diameter growth. When diameter growth exceeded 0.5 inch in 5 years, the mortality rate essentially leveled off without reaching zero. Tamarack and northern white-cedar were exceptions; these species had consistently low mortality at all growth levels.

There are four critical points where reliable mortality data are needed. Foremost is the mortality rate for "no growth" trees. If the data at this point need to be bolstered by including trees showing slight growth, then the estimate of mortality at no growth loses some reliability.

A second critical data point is the mortality rate for the fast-growing trees. For each species the most ample data appeared here.

At least two reliable data points between the nongrowers and the fast-growers are needed to establish the form of the mortality curve as mortality declines.

Mortality rates for at least the four critical diameter growth rates were established for all species except other red oaks, tamarack and northern white-cedar. With tamarack and northern white-cedar the relationship of mortality to diameter growth was not established because too few trees were available, especially too few slow or no growth trees. Therefore, a uniform mortality rate was assigned to all tamarack and another to northern white-cedar.

MODEL SELECTION

A mathematical expression for relating mortality to growth rate was sought for each species. The logistic function $Y = [1+\text{EXP}(\alpha+\sum\beta X)]^{-1}$ has been used effectively for modeling tree mortality (for example, Hamilton and Edwards (1976) and Monserud (1976) and for modeling human health risk (for example, Truett *et al.* (1967)).

Writing the logistic in terms of our application we have

$$R = [1+\text{EXP}(\alpha+\beta\bullet \text{DGR})]^{-1}, \qquad (2)$$

with DGR being the annual diameter growth rate.

Equivalent forms are $R' = \alpha'\ \text{EXP}\ (\beta\bullet \text{DGR})$ and $R' = \text{EXP}\ (\alpha+\beta\bullet \text{DGR})$, with $R' = (1 - R)/R$.

Three variations from this basic function (2) were also evaluated for usefulness in estimating mortality:

$$R = [1+\text{EXP}\ (\alpha+\beta\bullet \text{DGR})]^{-1} + \delta, \qquad (3)$$

$$R = [1+\text{EXP}\ (\alpha+\beta\bullet \text{DGR}^{\gamma})]^{-1}, \text{ and} \qquad (4)$$

$$R = [1+\text{EXP}\ (\alpha+\beta\bullet \text{DGR}^{\gamma})]^{-1} + \delta. \qquad (5)$$

Still another model was considered,

$$R = [1+\text{EXP}\ (\alpha+\beta\bullet \text{DGR}^{\gamma}+\omega\bullet \text{DBH})]^{-1} + \delta. \qquad (6)$$

to accommodate those species in which the effect of DGR depended upon tree size.

In these models, the parameter, α, establishes mortality at the no-diameter growth level with the very minor contribution of δ. DBH and its multiplier, ω, provide an adjustment based on tree size especially for trees having little or no growth. Inclusion of a background death rate, δ, provides for the occasional removal of a fast-growing tree. The progression of the mortality estimates from no-growth trees to that of fast growers is controlled by β and γ. Adding the exponent, γ, greatly increases the function's flexibility.

Model (6) was selected for seven of the species (table 3) and model (5) for the remainder. Estimates of the parameters under (5) are given for all species (table 4) to facilitate parameter comparison, even though (6) is the recommended model for seven species.

A preliminary screening of models (2) through (5), the first step in the selection process, was based on the ability of each to reproduce the mortality observed for each diameter-growth class. Inclusion of the background death rate (δ), models (3) and (5), greatly improved the estimates for annual growth rates in excess of 0.1 inch where a low, but non-zero, mortality rate was observed.

Table 3.— *Mortality function[1] for selected Lake States tree species (estimates based on diameter and diameter growth rate)*

Species	Parameters α	β	γ	ω	δ
Jack pine	0.3678	60.178	1.0727	0.12220	0.00502
Red pine	1.0843	11.012	.5887	.48500	.00020
Balsam fir	2.6976	30.550	.8996	-.23069	.00400
Basswood	-.5861	101.870	1.6493	.68398	.00489
Sugar maple	.8150	66.937	1.5934	.75000	.00435
Other red oaks	-1.1492	9.109	2.4552	.35000	.00000
Quaking aspen	-.0786	213.630	1.7126	.25812	.02276

[1] Estimated annual probability of a tree dying is $\{1/[1 + \text{EXP}\ (\alpha + \beta\cdot \text{DGR}^{\gamma} + \omega\cdot \text{DBH})]\} + \delta$ with DGR = diameter growth rate (inches per year) and DBH = diameter breast high.

The variable exponent for diameter growth rate (γ) yielded exponents less than 0.75 for three species, and more than 1.25 for 10 species (table 4)—a substantial departure from 1. In these instances model (5) more realistically portrayed the decline in mortality for trees with no growth to trees with 0.1-inch annual growth than did model (3).

Finally, model (5) could well be superior to the others eliminated at this point, yet still be deficient. Numerous questions come to mind. Is it applicable for all sites? Is it applicable over the geographic range of the species, for all stand densities, and for all diameters? And more.

One major evaluation was completed; estimated tree mortality was compared to mortality observed within each diameter class. To accomplish this, a two-way table was constructed having 1.0-inch diameter classes as one dimension and 0.02-inch annual growth classes as the other. Observed and estimated tree deaths along with total trees were calculated for each cell as well as for each diameter class and each diameter growth class.

Disagreement between observed and estimated tree deaths could be accepted, and was expected, within a diameter class. However, if these discrepancies formed a pattern whereby the estimated deaths were consistently too low for small trees and too high for large trees, or if the reverse pattern were true, then model (5) was deemed inadequate.

For six species, including red pine, balsam fir, basswood, sugar maple, other red oaks, and quaking aspen, model (5) overestimated mortality on the small trees and underestimated on the large. Jack pine revealed a modest reversal from this pattern. Model (6) adequately adjusted the estimated diameter class mortality patterns. Hence we used model (6) for these species.

Table 4.— *Mortality functions*[1] *for Lake States tree species (estimates based on diameter growth rate)*

	Parameters			
Species	α	β	γ	δ
Jack pine	1.2178	149.3669	1.3699	0.00856
Red pine	3.2185	17.3086	.6165	.00042
White pine	2.3507	33.6094	1.0088	.00201
White spruce	2.8806	30.7737	1.2309	.00396
Balsam fir	2.0754	29.5772	.9541	.00265
Black spruce	2.8774	432.9522	1.8576	.00235
Tamarack	13.0000[2]	1.0000	1.0000	.01334
N. white-cedar	13.0000[2]	1.0000	1.0000	.00402
Hemlock	2.8233	89.5603	1.0966	.00320
Black ash	1.4875	13.3384	.5429	.00018
Red maple	2.2405	53.5938	1.0392	.00494
Elm	1.9889	44.5414	1.0965	.00899
Yellow birch	2.6705	63.1477	1.3819	.00382
Basswood	2.2779	25.3602	.9027	.00317
Sugar maple	3.1831	82.5642	1.3605	.00405
White ash	1.7821	232.3075	1.7267	.00222
White oak	3.6946	95.6369	1.4517	.00188
S. red oak	2.3092	6,999.8220	2.6615	.00468
Other red oaks	1.0044	69.2301	1.8048	.00000
Hickory	3.0626	63.4946	1.0498	.00134
Bigtooth aspen	.8805	56.5925	1.2154	.01288
Quaking aspen	1.2199	693.5903	2.0753	.02384
Paper birch	2.1808	11.6263	.4750	.00029
Other hardwoods	2.2339	29.6290	1.3427	.00748
Noncommercial	2.3581	113.0644	.9993	.01923

[1] Estimated annual probability of a tree dying is $\{1/[1+\mathrm{EXP}(\alpha+\beta \cdot \mathrm{DGR}^{\gamma})\ ]\} + \delta$ with DGR = diameter growth rate (inches per year).

[2] Mortality is constant for all growth rates, relation to DGR not established, no slow-growing trees in sample.

VALIDATION

To evaluate model performance the mortality models were applied to two data sets that were not utilized in model development. One set consisted of 266 permanent plots from the Cloquet Experimental Forest, Carlton County, Minnesota; the Forest is managed by the College of Forestry, University of Minnesota. These plots provided test data primarily for aspen, birch, and northern conifers (table 5). An initial measurement and three remeasurements, spanning a period of 17 years, were available.

The second set consisted of 38 permanent plots from the Dukes Experimental Forest, Marquette County, Upper Michigan. The Dukes Forest is managed by the North Central Forest Experiment Station. These plots provided a small set of test data for northern hardwoods (table 5). An initial measurement and two remeasurements, spanning a period of 10 years, were available.

One validation consisted of comparing the number of trees, by species, expected to die during the status observation interval with those actually dying in the interval. With this, the probability of death was determined for each tree of the species using that species' mortality model. As in the model derivation process, diameter growth rate was based on the first two diameter measurements for a tree, and the status was observed at the third measurement. The count of trees observed to die was compared to expected deaths based on the model (table 5).

The largest discrepancy between actual tree deaths and model estimates was for jack pine. Excessive deaths were yielded by the model, especially for trees growing less than 0.08 inch per year, and for trees less than 8.6 inches in diameter. The tamarack and quaking aspen models also overestimated mortality, though the aspen differences were not large.

Table 5.— *Observed and estimated tree mortality on validation plots by tree species*

Species	CLOQUET PLOTS: Initial measurement through second remeasurement[1]: Trees in test	Mortality: Observed	Mortality: Estimated	First remeasurement through third remeasurement[2]: Trees in test	Mortality: Observed	Mortality: Estimated
Jack pine	1,674	111	211	1,597	207	278
Red pine	899	3	5	1,032	6	17
White pine	170	11	6	185	20	9
White spruce	69	6	4	104	0	6
Balsam fir	513	73	65	613	130	94
Black spruce	778	54	55	832	118	81
Tamarack	300	6	19	318	16	29
N. white-cedar	354	7	7	394	16	11
Ash	61	1	5	76	13	8
Red maple	75	0	3	93	8	5
Bigtooth aspen	53	8	10	50	10	14
Quaking aspen	611	89	103	653	166	174
Paper birch	800	8	12	889	39	24
DUKES PLOTS[3]						
Elm	71	1	4	—	—	—
Basswood	67	1	2	—	—	—
Sugar maple	400	5	6	—	—	—

[1] Diameter growth rate based on 5 years' growth, status observed 5 years later.
[2] Diameter growth rate based on 5 years' growth, status observed 7 years later.
[3] Diameter growth rate based on 7 years' growth, status observed 3 years later.

Numerous species, including white spruce, northern white-cedar, bigtooth aspen, elm, basswood, and sugar maple, showed good agreement between actual and estimated mortality. With the exception of 10 predicted deaths among the 148 1-inch trees (none were found), the red pine estimates were good. Ash and red maple showed variation in results between observation periods, but on balance yielded good results.

Mortality was underestimated for white pine, primarily with the 6-inch trees; for balsam fir and black spruce, primarily with the 5-, 6-, and 7-inch trees; and for paper birch.

The second validation consisted of simulating mortality for each plot, paralleling the use of mortality models in stand growth simulation. Based on random selection in proportion to each tree's likelihood of death, each tree was assigned either a mortality or a survivor status. A count of these mortality trees provided an estimate of plot mortality through simulation for comparison with observed plot mortality.

To arrive at the probability associated with each mortality count, each tree on a plot was given 100 assignments of 1 (mortality tree) or 0 (survivor tree). This was done through generating 100 random numbers between 0 and 1 for each tree and comparing each number with the tree's likelihood of death. If the random number did not exceed this likelihood, the tree was assigned a status of 1, death. Otherwise the tree was scored 0, a survivor tree.

The first scores were added for all trees on the plot to arrive at one mortality count for the plot. This process was repeated for each of the 99 remaining scores. A distribution of these 100 counts was made for each plot, providing a relative frequency or probability for each mortality count.

Consider the results from Cloquet plot 82 (table 6). This plot had 30 trees with two diameter measurements. When status was recorded 5 years later, one dead tree was found. Expected mortality using the mortality functions for the species present was 0.94. On this plot the probability of selecting exactly one tree to die in the 5-year interval based on 100 applications of the selection process was 0.30, i.e., 30 of the 100 simulation runs produced exactly one dead tree. The probability of selecting either zero, one, or two trees, a count within one of the observed mortality, was 0.91.

Ten Cloquet plots demonstrate the discrepancies that might be encountered in stand growth simulation (table 6). These plots were selected because of their close agreement between observed and expected mortality. Still, the highest proportion of hits, simulation results equal to observed mortality, was the 0.47 (47 of the 100 simulation

Table 6.—*Relative frequencies (probabilities) of mortality tree counts for 10 Cloquet plots determined by random selections in proportion to each tree's probability of dying in 5 years (basis: 100 sets of tree counts per plot)*

		Mortality trees		**Mortality tree counts**													
Plot	**Trees**	**Observ.**	**Exp.**[1]	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Number																	
82	30	1	0.94	.43	.30	.18	.08	.01	—	—	—	—	—	—	—	—	—
68	19	1	1.01	.36	.42	.17	.05	—	—	—	—	—	—	—	—	—	—
237	30	1	1.00	.34	.47	.16	.03	—	—	—	—	—	—	—	—	—	—
4	36	2	1.55	.26	.28	.27	.15	.02	.01	.01	—	—	—	—	—	—	—
398	18	2	2.43	.01	.18	.40	.18	.16	.05	.02	—	—	—	—	—	—	—
147	53	3	3.48	.02	.10	.12	.25	.17	.15	.10	.07	.02	—	—	—	—	—
111	33	4	4.63	.01	.01	.11	.13	.21	.24	.17	.08	.02	.02	—	—	—	—
285	29	5	4.65	—	.02	.11	.17	.23	.21	.13	.06	.05	.02	—	—	—	—
177	36	5	4.92	—	.01	.05	.12	.21	.23	.21	.14	.02	.01	—	—	—	—
204	45	7	7.88	—	—	.01	—	.02	.13	.18	.17	.16	.17	.10	.03	.02	.01

[1] Expected mortality is the sum of the tree probabilities of dying over 5 years.

runs produced one dead tree each) found for plot 237. Plot 177, with observed mortality at five trees and expected at 4.92, showed only 23 hits in 100 applications.

Clearly, the mortality counts from stand growth simulation will often differ from the actual, even when the model is appropriate. However, the demonstration material (table 6) indicates we can expect to be within one tree of the true count most of the time.

The Cloquet and Dukes plots having at most one mortality tree were summarized on the basis of conformity between each plot's observed mortality and the results from mortality simulation (table 7). On four plots (Cloquet plots having 11 or more trees, one with no mortality and three with one mortality tree each) the probability of getting the correct mortality count through simulation was zero. At the other extreme, 26 of the Cloquet plots having 10 or fewer trees and no mortality showed probability of 0.91 to 1.0 of getting the correct mortality through simulation.

Except for plots having 10 or fewer trees and no mortality, most plots did not have a high probability of hitting the observed mortality through mortality simulation. However, most plots met the relaxed criterion of being within one tree of the correct number.

Only 31 of the 87 Cloquet plots with two or more mortality trees had a probability exceeding 0.20 of producing the correct mortality count through simulation (table 8). Furthermore, the criterion of being within one tree of the correct count was not met consistently by plots having three or more mortality trees.

Thirteen plots containing 11 or more trees each had zero probability of producing the correct mortality count through simulation. Of these, 11 had mortality counts in excess of the observed mortality, and two were less than the observed mortality. Jack pine was the prime contributor to nine of the plots having excessive counts.

Table 7.— *Probability of conformity by plot between mortality tree counts determined by random selections in proportion to each tree's probability of dying (simulation) and observed counts for each plot having at most one mortality tree (basis: 100 sets of simulation tree counts per plot)*

	(Number of plots)											
	Cloquet plots								Dukes plots[2]			
	Plots: 10 or fewer trees				Plots: 11 or more trees							
Probability	Mortality (0)[1]		Mortality (1)		Mortality (0)		Mortality (1)		Mortality (0)		Mortality (1)	
	Hit[3]	Within 1 tree	Hit	Within 1 tree	Hit	Within 1 tree	Hit	Within 1 tree	Hit	Within 1 tree	Hit	Within 1 tree
.00					1		3	2				
.01-.10			3		13	2	5	2	1		1	
.11-.20			2		8		5	1				
.21-.30			2		6	5	7	2	1		2	
.31-.40			1		5	5	11		2		2	
.41-.50	3		2		5	5	5	4	2	1		
.51-.60	1				5	4		2	4			
.61-.70	2				6	5		3	7	1		
.71-.80	6	1			10	5		2	5	4		
.81-.90	16	3	1		4	11		5	8	3		
.91-1.0	26	50		11	8	29		13	2	23		5
Total plots	54	54	11	11	71	71	36	36	32	32	5	5

[1] No mortality observed on these plots.

[2] One plot with two mortality trees not included.

[3] The simulation count for the plot is the same as the observed mortality.

Table 8.— *Probability of conformity by plot between mortality tree counts determined by random selections in proportion to each tree's probability of dying (simulation) and observed counts for each Cloquet plot having two or more mortality trees (basis: 100 sets of simulation tree counts per plot)*

	(Number of plots)											
	Plots: 10 or fewer trees			Plots: 11 or more trees								
	Mortality (2 or 3)[1]			Mortality (2)			Mortality (3)			Mortality (4 or more)		
Probability	Hit[2]	Within 1 tree	Within 2 trees	Hit	Within 1 tree	Within 2 trees	Hit	Within 1 tree	Within 2 trees	Hit	Within 1 tree	Within 2 trees
.00	2			2			4	2	1	3	1	1
.01-.10	5	1		3	2	1	6	3	2	15	5	
.11-.20	1	1		9	1	1	3	1		3	5	3
.21-.30	3	3		10	1		5	2	1	7	5	4
.31-.40		2		5	2	1	1	3	1		4	1
.41-.50					1			2	2		1	4
.51-.60		1			3	1		2	1		5	3
.61-.70					12	1		3	2		2	5
.71-.80		2			5			1	3			1
.81-.90					2	5			4			4
.91-1.0		1	11			19			2			2
Total plots	11	11	11	29	29	29	19	19	19	28	28	28

[1] Either two or three mortality trees observed on these plots.

[2] The simulation count for the plot is the same as the observed mortality.

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TIMBER MANAGEMENT GUIDES AND MARKING RULES[1]

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Previous papers have described a forest growth projection system capable of "growing" and "killing" trees. Because it does not select trees for removal, the system applies only to **unmanaged** stands. To accurately project **managed** stands a procedure is needed that will remove trees (simulate cutting) according to prescribed guidelines. This paper describes the procedure (algorithm) used to simulate tree removals recommended in management guides, and indicates some possible uses for the projection system with the addition of the algorithm. FORTRAN subroutines called by the projection system computer program (Hahn and Brand 1979) implement the tree removal algorithm.

DESCRIPTION OF THE SILVICULTURAL ALGORITHM

The algorithm has three major parts. Because different species produce different products, mature at different ages, and grow under different conditions, the guides used by forest managers are species dependent, and are therefore developed for specific cover types. In the projection system a tree list characterizes the portion of the forest of interest (Leary 1979). The first part of the algorithm determines, on the basis of this tree list, the cover type—and thus, the most appropriate guide to use. The selected guide, along with plot values, determine a silvicultural action to be carried out on the tree list. The final part of the algorithm performs the suggested action.

Cover type may be determined by the species with the greatest number of stems, number of dominant and codominant stems, basal area, basal area of dominants and codominants, or some other method. The Society of American Foresters (1954) favors using the number of dominant and codominant stems. The USDA Forest Service (1974) states that cover type should be based on species most fully occupying the area. The latter point indicates that tree size as well as number is important. Since crown class cannot be projected by the model, a classification based on crown position is impractical. To incorporate size into the procedure, basal area rather than total stems was used to determine cover type. An algorithm used by North Central Forest Experiment Station Forest Survey [2] is the basis for determining the type.

SELECTING THE ACTION

In most cases, guides prepared by North Central Forest Experiment Station silviculturists were used to develop the algorithms. Each guide was translated to a diagram that systematically evaluates stand characteristics to reach a final recommendation. The sources for the diagrams are as follows:

Cover type	*Source*
Jack pine	Benzie (1977a)
Red pine	Benzie (1977b)
White pine	USDA Forest Service (1958)
Spruce-fir	USDA Forest Service (1967a)
Black spruce	Johnston (1977a)
Northern white-cedar	Johnston (1977b)
Mixed swamp conifers	Johnston (1977b)
Lowland hardwoods	Godman (personal communication)

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[1] *This work was conducted under a cooperative agreement between the North Central Forest Experiment Station and the College of Forestry, University of Minnesota, St. Paul, Minnesota.*

[2] *Hahn, J. T. Personal communication, 1976.*

Northern hardwoods	Tubbs (1977), Godman (personal communication)
Oak-hickory	Sander (1977)
Aspen-paper birch	Perala (personal communication) USDA Forest Service (1967b)
Understocked stands of above cover types	Benzie (personal communication)

Cover Typing

The purpose of the typing algorithm is to determine the most appropriate cover type and therefore the correct guide for evaluating the tree list. Most tree lists will have a cover type assigned to them that was either determined in the field or by computer analysis. In either case, there are advantages to determining cover type directly from the tree list using a computer algorithm. One is that it will ensure that identical tree lists have the same cover type regardless of their source. It also allows the cover type to change with projected composition changes.

These guides have several advantages over other possible guides. They enjoy rather widespread use in the Lake States and thus it is more likely that region-wide projections will be accurate. They exist for the major timber types in the Lake States, so there is some consistency. And finally, they do not recommend actions so intensive that the model cannot respond to them. For example, fertilization could not be adequately represented by the model because coefficients are not available to predict growth responses to fertilization.

Since management guides are interpreted by oresters in the field, professional judgment can nfluence the choice of a final action. To use computer methods in determining an action requires decisions using a tree list that does not contain all the information available in the field. As a result, ome simplifying assumptions had to be made in onstructing algorithms for the various types. These assumptions were checked with silviculturists and appear to be reasonable.

Various actions are suggested by the guides ich as "do nothing," "clearcut", "thin", "shelterood cut", and "remove overtopping trees". The ecommended actions are based on site quality, stand characteristics, and cover type. For example, clearcutting is prescribed in a jack pine stand if the site index is 60 and stand age is 65 years. Clearcutting in an aspen stand, however, is prescribed if the stand age is 35 years.

Decision diagrams containing these criteria were produced for each type. Stand and site characteristics are used to guide decisions in the diagrams, which are constructed along the lines of a taxonomic key (fig. 1). For example, assume a jack pine tree list has the following stand characteristics: average stand diameter—5 inches; basal area—100 square feet/acre; site index—50 feet; stand age—35 years; number of trees—500/acre; and BAMIN—55.6 square feet/acre (BAMIN is the amount of basal area needed to achieve full stocking.). The dashed line in figure 1 indicates how a final recommendation would be reached. Since average stand diameter is 5 inches, the bottom branch is followed. Again the bottom branch is taken since the basal area is greater than 55.6 square feet per acre. The site index and age indicate that the top branches are now appropriate, leading to the final recommendation, "do nothing".

A disadvantage of this approach is that it lacks flexibility—only this decision diagram can be used for jack pine. To allow more flexibility, the critical values are read as input variables and can therefore be changed. Figure 2 shows the more general form of the decision diagram for jack pine. Now, by selecting JP(7) as 50 years and the rest equal to zero, jack pine can be managed on a 50-year rotation with no intermediate cutting. The guides can be manipulated to test the effect of different maximum and residual basal areas, different rotation ages, or less intensive management.

Marking

After an action has been selected according to the guide, it must be carried out. The marking part of the algorithm selects trees for removal according to tree characteristics. In the simple case of clearcutting, all live trees are "marked" as cut. For more complicated actions, such as thinning, characteristics must be selected that allow ranking of trees for desirability of removal. Low-preference trees are marked for cutting until the required residual stand is achieved.

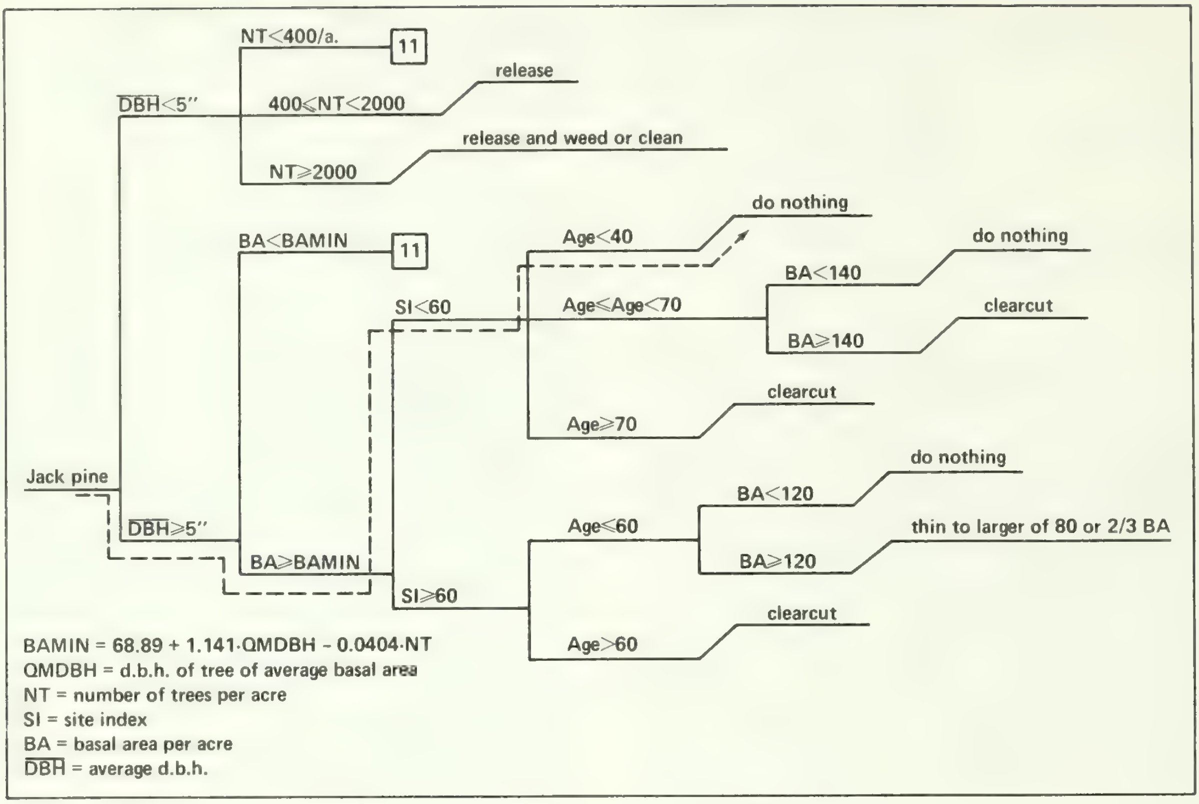

Figure 1.—*Specific jack pine decision diagram.*

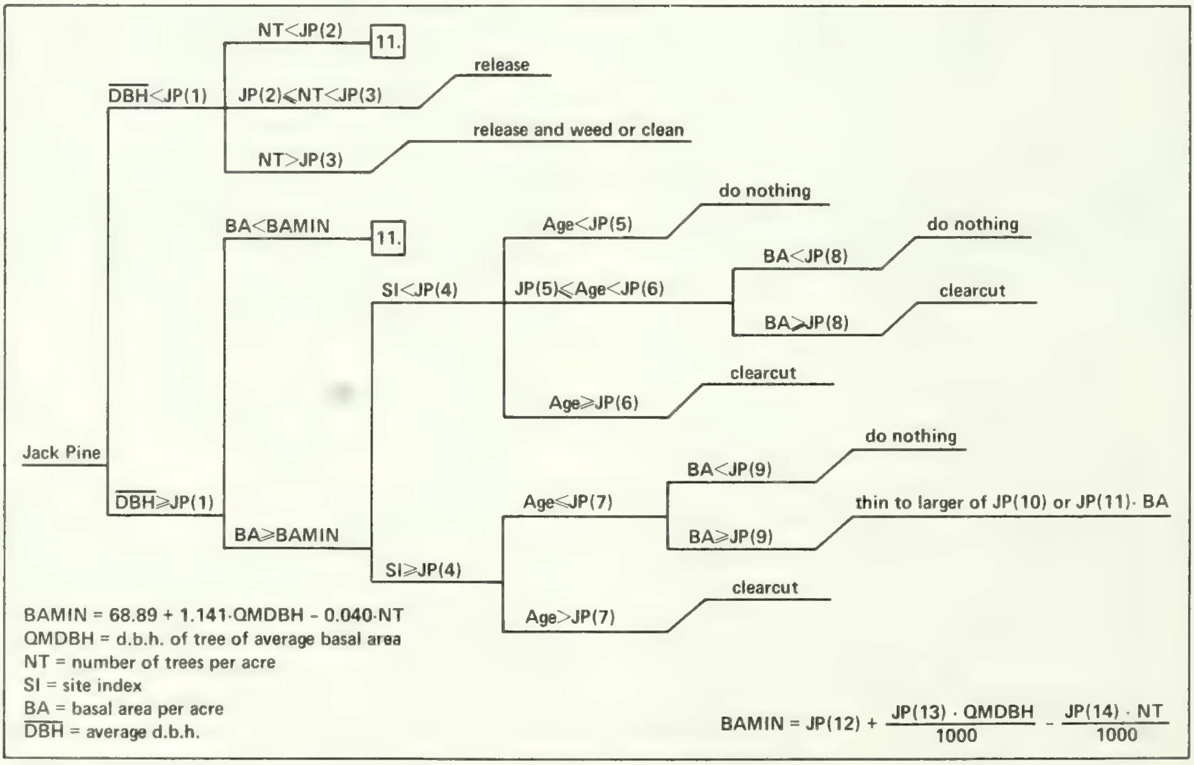

Figure 2.—*Generalized jack pine decison diagram.*

The various removal procedures used to carry out specified actions are listed below:

Removal procedure	*Input needed*
1. rough and rotten	size class to remove
2. small trees, unspecified species	size class to remove four species to leave
3. large trees, unspecified species	size class to remove four species to leave
4. small trees, specified species	size class to remove four species to remove
5. large trees, specified species	size class to remove four species to remove
6. shelterwood cut	size class to remove four species to favor
7. reduce number of trees	number of trees to leave
8. all overtopping	lowest d.b.h. of trees to remove
9. all trees of a certain size and species	size class to remove four species to remove

The removal procedures have been selected to accomplish all the final actions recommended by the management guides. For instance, jack pine stands less than 60 years old with 120 square feet of basal area per acre and a site index greater than 60 should be thinned from below to 80 square feet per acre. The first, second, and fourth procedures will accomplish this action. Rough and rotten trees are removed first, and if the basal area is still too high, the smallest tree of an undesirable species is removed. When all undesirable species are removed and the residual stand has still not been achieved, the smallest trees of desirable species are removed. Marking is discontinued when the residual basal area is achieved.

As with action selection, it is desirable to have the ability to change the marking rules. To permit his flexibility, different hierarchies of removal rocedures may be selected. This option permits up to five of the removal procedures listed above to e selected for each recommended action. Returnng to the jack pine example—by selecting the rst, third, and fifth removal procedures the stand an be thinned in such a way that the largest trees re removed first.

RELATIONSHIP TO THE REST OF THE PROJECTION SYSTEM

Because effective use of the management guide algorithm depends on the rest of the projection system, it is important to present a simplified description of how the pieces interrelate. A tree list (representing a stand) is brought into the system and its cover type and silvicultural action are determined as previously described. The action is carried out and the appropriate trees are coded as cut. One year's growth is determined for the remaining trees and the mortality function applied. Trees are coded as dead if selected by the mortality function. The revised tree list is cycled through the growth and mortality functions to determine annual changes until the desired number of years between cutting cycles has occurred. Cover type, silvicultural action, and trees to mark are again determined using the current tree list. This procedure continues until the tree list has been projected for the desired number of years. (If another stand (tree list) is to be projected, the new tree list is brought into the system and the entire cycle is repeated.)

POSSIBLE USES

Incorporation of the management algorithms into the projection system makes possible several additional uses of the system. Survey information, in the form of tree lists, is available on a statewide basis. Applying the projection system to these tree lists would produce timber yields expected from the state if all lands were managed according to the guides. Comparison with present yields would indicate the intensity of management as well as opportunities for increasing timber yields.

Another use for the system would be testing various management guides and marking rules. Actual or contrived tree lists could be projected using different guides, and the yields then compared. This would provide a much faster means of comparing alternatives and help identify those most promising for field testing. By experimenting with marking rules, the effect on timber yields of leaving rough and rotten trees as den trees or favoring different species or size classes could be determined. Comparing these yields with those obtained from the original marking rules would be a meaure of the "cost" of the new marking rule.

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AN IMPLEMENTATION PROGRAM

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The various parts of the generalized forest rowth projection system have been described lsewhere (Buchman 1979, Christensen *et al.* 1979, eary, *et al.* 1979, Hahn and Leary 1979, Leary nd Holdaway 1979, Brand 1979). TRES (Timber esource Evaluation System) is the computer pro-ram that combines the parts into a package capa-le of simulating the growth of trees entered into he system. This paper is not intended to be a etailed user's guide, but rather a general descrip-ion of the input needed, how the parts are put ogether, and the output produced.

INPUT

The input consists of a parameter deck and a ree list. A tree list consists of tree species, d.b.h., rown ratio, and quality class for a group of trees. lso required are site index, stand age, and plot ze.

Parameter Deck

The parameter deck specifies two groups of in-ut values: user-selected options, and numerical nstants needed by each portion of the growth rocessor.

Numerical constants are used for:

(1) assigning species group codes to individual trees,
(2) crown ratio function coefficients,
(3) silvicultural treatment specifications,
(4) volume equation coefficients,
(5) mortality equation coefficients,
(6) potential growth function coefficients,
(7) growth modifier coefficients,
(8) allocation rule coefficients, and
9) a species grouping priority matrix (used for combining species when more than three species occur on a plot).

These values are determined from calibrating the model on a specific data base of permanent (remeasured) plots.

Projection related options that may be selected by the user are:

(1) length of projection cycle (years),
(2) number of projection cycles, and
(3) type of growth projection desired (validation, projection, or update).

The number of years the tree list is projected is determined by the number and length of the cycles. The projection is limited to a maximum of 100 years, but it may be in the form of 100 cycles of 1 year each or one cycle of 100 years. The length of the cycle determines how often summaries are made and the tree list examined for management opportunities.

Three types of growth projections can be selected: validation, projection, and update. A validation run uses a tree list with measurements recorded for several different years. The tree list is projected from the initial measurement to the final measurement. Projected and actual measurements are compared to determine the accuracy of the model. A projection run starts with initial conditions and grows the trees for a specified length of time to estimate future conditions. Finally, an update run starts with initial conditions from the past and grows the trees to the present. Using known product removals, the trees that produced those products are removed from the tree list. This update section of the program is currently being developed. An example of an echo of the input for a validation run appears in Appendix A.

Tree List

Regardless of whether the tree list comes from sample plots or is derived (for example, from a stand table), the tree list can be in one of three forms. The first is a list in the format described by Christensen *et al*. (1979). The second is tree information in the unit record format used by the USDA Forest Service Renewable Resources Evaluation (forest survey) projects. And finally, a tree list in a computer-readable format specified by a user may be selected, in which case the user is responsible for supplying the necessary computer code for input and output routines.

PROGRAM ORGANIZATION

Besides providing input/output capability, the program controls when the different parts of the system are used according to the options selected. Table 1 gives a listing of all the subroutine and function names, their calling routines, and a brief statement of their purpose. The program has seven parts:

(1) the main calling program,
(2) a function, VALUE, where all mathematical equations are located,
(3) input subroutines,
(4) a subroutine for aggregating the input tree list,
(5) stand treatment subroutines,
(6) stand growth subroutines, and
(7) output subroutines.

Figures 1 to 7 contain flow charts for each of the seven parts. Figure 1 shows the structure of the main calling routine and figure 2 the structure of the function VALUE.

Figure 3 shows the set of subroutines for reading the input parameters and the tree list. The structure of subroutine READ is shown in figure 3a. It reads input parameters and echo-prints all values. Figure 3b shows the subroutine structure for reading tree lists in master format (Christensen *et al*. 1979); figures 3c and 3d show subroutine structure for reading tree lists in Renewable Resources Evaluation (forest survey) unit record format. The possibility of a user-written subroutine is indicated by figure 3e.

When all input (parameters and tree list) has been read, the tree list is partitioned into species groups and size classes by subroutine FIT (fig. 4), called from the main program TRES (fig. 1).

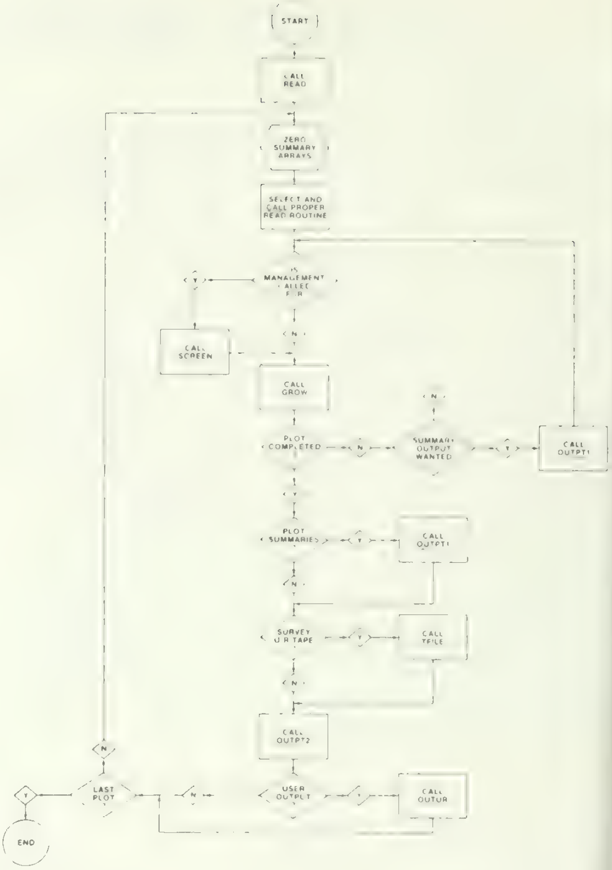


Figure 1.—Main program calling **TRES.**

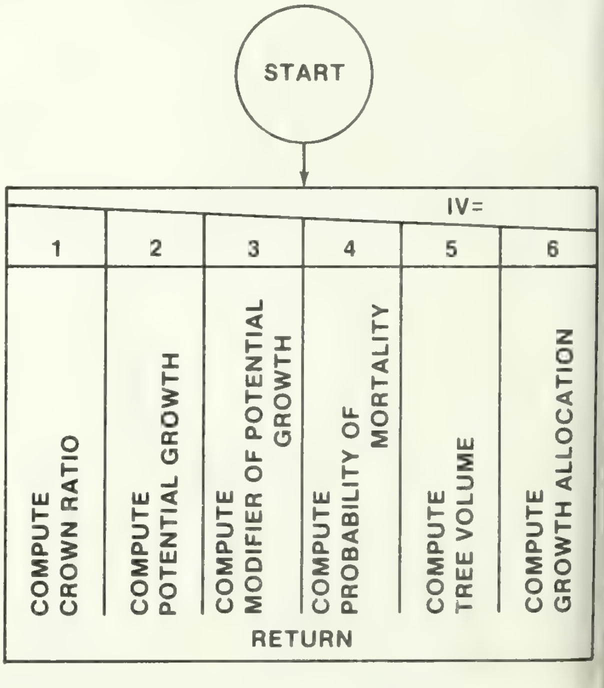

START
IV=
1
2
3
4
5
6
COMPUTE CROWN RATIO
COMPUTE POTENTIAL GROWTH
COMPUTE MODIFIER OF POTENTIAL GROWTH
COMPUTE PROBABILITY OF MORTALITY
COMPUTE TREE VOLUME
COMPUTE GROWTH ALLOCATION
RETURN

Figure 2.—Function **VALUE.**

Table 1.—*Subsystem TRES (Timber Resource Evaluation System) of program FREP (Forest Resources Evaluation Program)*

	Part Function
Program TRES Main calling routine. Sets up and initializes arrays, performs housekeeping functions, organizes calling of subroutines.	1. Main Program
Function VALUE Called from RMASTR, RSURTP, GROW, ISUM, OUTPTI, and OUTPUT2. Computes values for crown ratio, potential growth, modifier, mortality, volume, and growth allocation functions.	2. Mathematical functions
Subroutine READ Called from TRES. Reads user-selected options and numerical constants and echo-prints all values. *Subroutine RMASTR* Called from TRES. Reads data from binary files in MASTER format into arrays TRS and ITRS. Initializes array parameters. *Subroutine RSURTP* Called from TRES. Reads data from files in forest survey unit record format into arrays TRS and ITRS. Initializes array parameters. *Subroutine OPENRD* Called from RSURTP. Unblocks forest survey unit record file and supplies one record at a time to RSURTP. Has entry point READIT. *Subroutine RUSER* Called from TRES. Supplied by user to read user dat file into arrays TRS and ITRS.	3. Input
Subroutine FIT Called from TRES, SCREEN and REMOVE. Classifies trees in arrays TRS-ITRS into projection groups.	4. Aggregation of species
Subroutine SCREEN Called from TRES. Screens plots for possible treatment and/or sets up treatment schedule. *Subroutine COVTYPE* Called from SCREEN. Determines cover type using live trees in tree list. *Subroutine TREAT* Called from SCREEN Performs silvicultural treatments prescribed in SCREEN.	5. Stand treatments
Subroutine GROW Called from TRES. Grows trees, selects trees for mortality, allocates growth to individual trees, updates TRS and ITRS array. *Subroutine REMOVE* Called from GROW. Removes trees to meet specified annual removals for updates or trees recorded as having been removed by remeasurements. *Subroutine ISUM* Called from GROW, OUTPTI, TRES Summarizes trees into classification groups and computes group totals.	6. Stand growth
Subroutine OUTPTI Called from TRES. Outputs summaries for specified points in time. *Subroutine TFILE* Called from TRES. Outputs updated forest survey unit record file. *Subroutine OPENWR* Called from TFILE. Writes blocked unit record tape Has entry points WRITIT and CLOSWR. *Subroutine OUTPT2* Called from TRES. Outputs file for validation tests. *Subroutine OUTUR* Called from TRES. Supplied by user to output updated tree list to user specifications.	7. Output

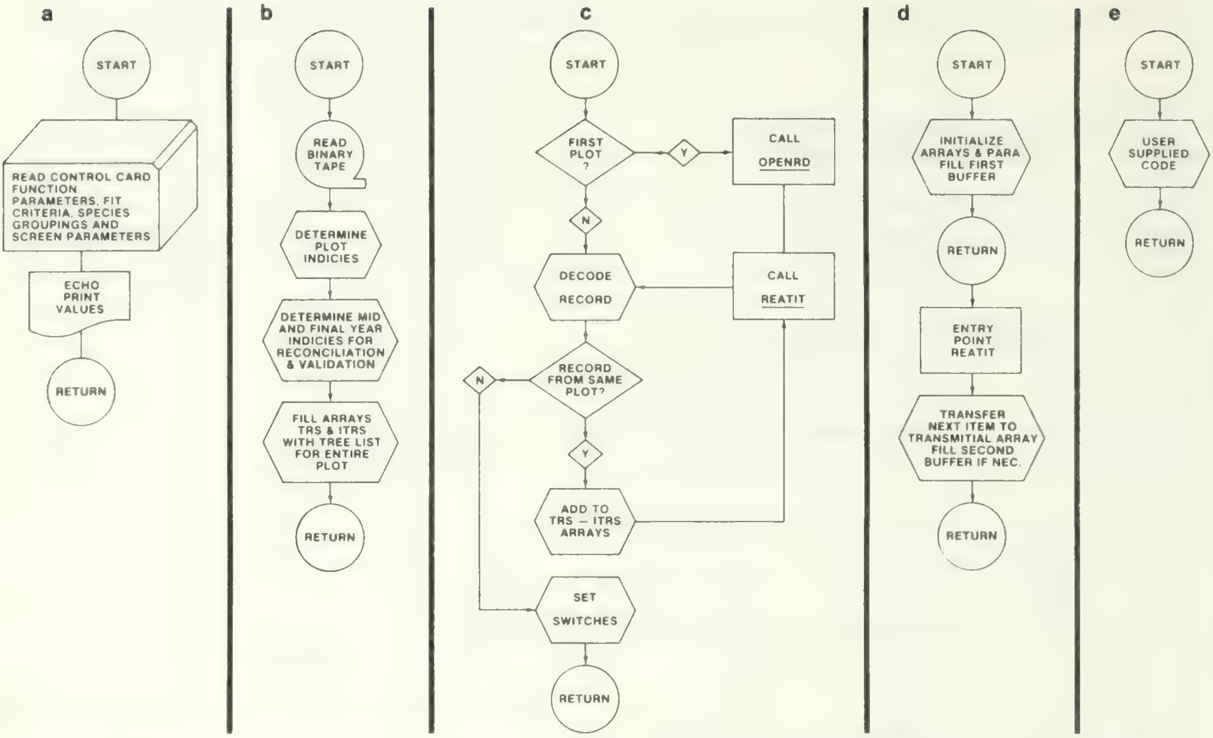

a
START
READ CONTROL CARD FUNCTION PARAMETERS, FIT CRITERIA, SPECIES GROUPINGS AND SCREEN PARAMETERS
ECHO PRINT VALUES
RETURN
b
START
READ BINARY TAPE
DETERMINE PLOT INDICIES
DETERMINE MID AND FINAL YEAR INDICIES FOR RECONCILIATION & VALIDATION
FILL ARRAYS TRS & ITRS WITH TREE LIST FOR ENTIRE PLOT
RETURN
c
START
FIRST PLOT ?
Y
CALL OPENRD
N
DECODE RECORD
CALL REATIT
N
RECORD FROM SAME PLOT?
Y
ADD TO TRS – ITRS ARRAYS
SET SWITCHES
RETURN
d
START
INITIALIZE ARRAYS & PARA FILL FIRST BUFFER
RETURN
ENTRY POINT REATIT
TRANSFER NEXT ITEM TO TRANSMITIAL ARRAY FILL SECOND BUFFER IF NEC.
RETURN
e
START
USER SUPPLIED CODE
RETURN

Figure 3.—Subroutines (a) **READ,** *(b)* **RMASTR,** *(c)* **RSURTP,** *(d)* **OPENRD,** *and (e)* **RUSER.**

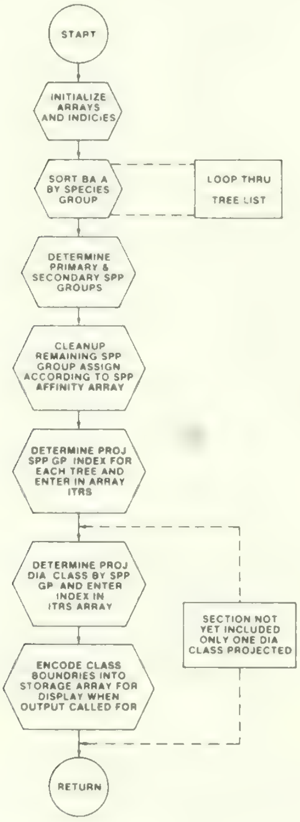

START
INITIALIZE ARRAYS AND INDICIES
SORT BA A BY SPECIES GROUP
LOOP THRU TREE LIST
DETERMINE PRIMARY & SECONDARY SPP GROUPS
CLEANUP REMAINING SPP GROUP ASSIGN ACCORDING TO SPP AFFINITY ARRAY
DETERMINE PROJ SPP GP INDEX FOR EACH TREE AND ENTER IN ARRAY ITRS
DETERMINE PROJ DIA CLASS BY SPP GP AND ENTER INDEX IN ITRS ARRAY
SECTION NOT YET INCLUDED ONLY ONE DIA CLASS PROJECTED
ENCODE CLASS BOUNDRIES INTO STORAGE ARRAY FOR DISPLAY WHEN OUTPUT CALLED FOR
RETURN

Figure 4.—Subroutine **FIT.**

Selecting the option to manage the stand as it being projected, following the management guid of Brand (1979), causes subroutines SCREE COVTYPE and TREAT to be called. Figure shows the flow chart of SCREEN, from whi COVTYPE and TREAT are called. COVTYP (fig. 5b), which is also called at the end of a pr jection by OUTPUT2, determines the cover typ TREAT (fig. 5c) performs the silvicultural trea ments selected in SCREEN. Trees selected for r moval are designated as cut, and the live trees a again divided into species and diameter groups a recall of subroutine FIT. This allows the chang in species composition caused by cutting to modi the numerical constants used to project the plo

The tree list is projected 1 year at a time for t number of years in a cycle and for the number cycles in the run by subroutine GROW, REMOV and ISUM (fig. 6). A plot is then projected throu the end of projection period; it cannot be revisit until all plots have been processed. The cro ratio function (Holdaway *et al.* 1979), potent growth function (Hahn and Leary 1979), and m ifier function (Leary and Holdaway 1979) are us to determine total growth of each diameter/species projection group (fig. 6a). Individual tree growth is then determined from the growth allocation function (Leary *et al.* 1979). Mortality trees are determined using the mortality function (Buchman 1979) and pseudo-random number generator.

OUTPUT

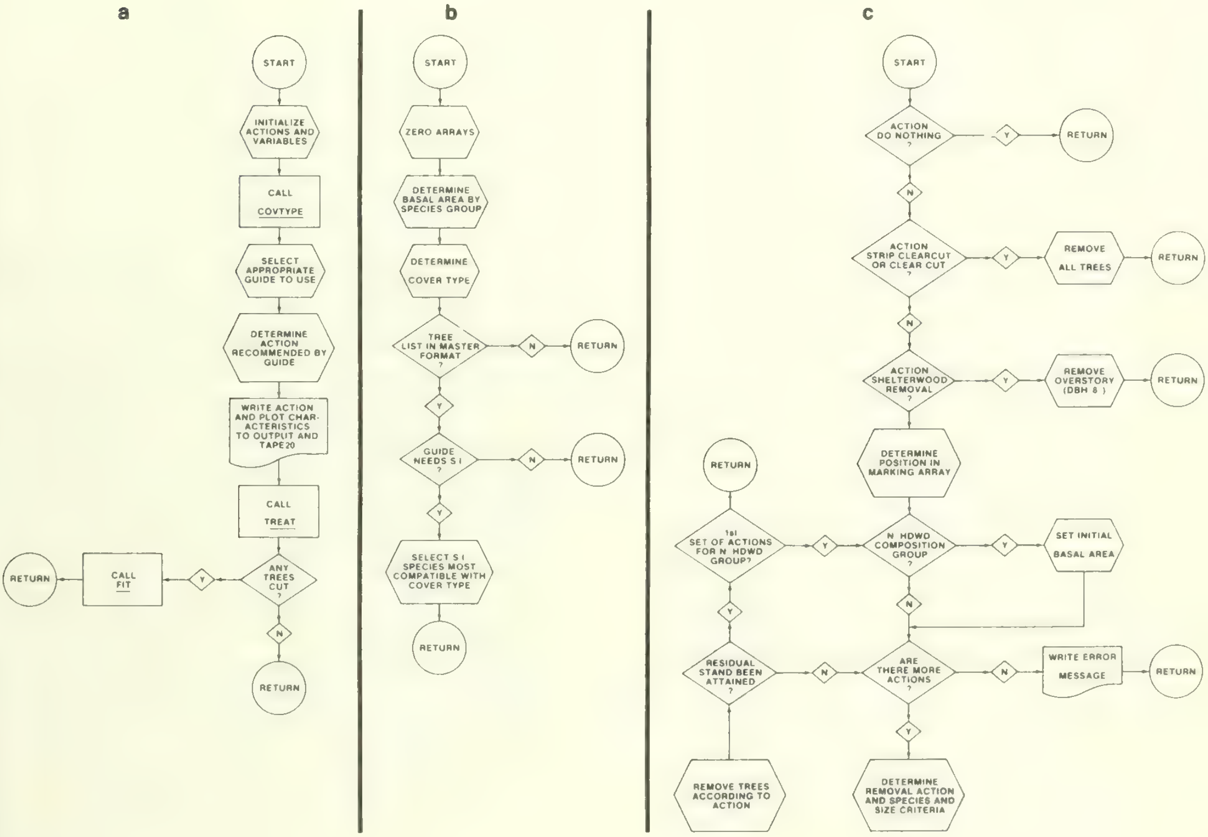
Four different output types are possible:

(1) "Yield table" output containing such variables as basal area and number of mortality trees, surviving trees, basal area and sum of diameters on a per plot and per acre basis, and cut tree volumes on a per acre basis. This output is given by subroutine OUTPTl (fig. 7a) and is available at the end of each cycle as well as at the beginning and end of the projection period. Appendix B shows an example of this form of output.

(2) A new Renewable Resources Evaluation (forest survey) unit record file (subroutine TFILE and OPENRD, figs. 7b and 7c respectively).

(3) A file for validating the projection system. This is produced by subroutine OUTPT2 (fig. 7d) and has meaning only if two or more measurements have been made on the plot. The file produced by OUTPT2 is ordinarily stored on disk and analyzed by a separate user-written program.

(4) A user-designed output file (subroutine OUTUR, fig. 7c).



a
START
INITIALIZE ACTIONS AND VARIABLES
CALL COVTYPE
SELECT APPROPRIATE GUIDE TO USE
DETERMINE ACTION RECOMMENDED BY GUIDE
WRITE ACTION AND PLOT CHARACTERISTICS TO OUTPUT AND TAPE20
CALL TREAT
ANY TREES CUT ?
Y
CALL FIT
RETURN
N
RETURN
b
START
ZERO ARRAYS
DETERMINE BASAL AREA BY SPECIES GROUP
DETERMINE COVER TYPE
TREE LIST IN MASTER FORMAT ?
N
RETURN
Y
GUIDE NEEDS S I ?
N
RETURN
Y
SELECT S I SPECIES MOST COMPATIBLE WITH COVER TYPE
RETURN
c
START
ACTION DO NOTHING ?
Y
RETURN
N
ACTION STRIP CLEARCUT OR CLEAR CUT ?
Y
REMOVE ALL TREES
RETURN
N
ACTION SHELTERWOOD REMOVAL ?
Y
REMOVE OVERSTORY (DBH 8)
RETURN
DETERMINE POSITION IN MARKING ARRAY
N HDWD COMPOSITION GROUP ?
Y
SET INITIAL BASAL AREA
N
RETURN
1st SET OF ACTIONS FOR N HDWD GROUP?
Y
Y
RESIDUAL STAND BEEN ATTAINED ?
N
ARE THERE MORE ACTIONS ?
N
WRITE ERROR MESSAGE
RETURN
Y
REMOVE TREES ACCORDING TO ACTION
DETERMINE REMOVAL ACTION AND SPECIES AND SIZE CRITERIA

Figure 5.—Subroutines (a) **SCREEN,** *(b)* **COVTYPE,** *and (c)* **TREAT.**

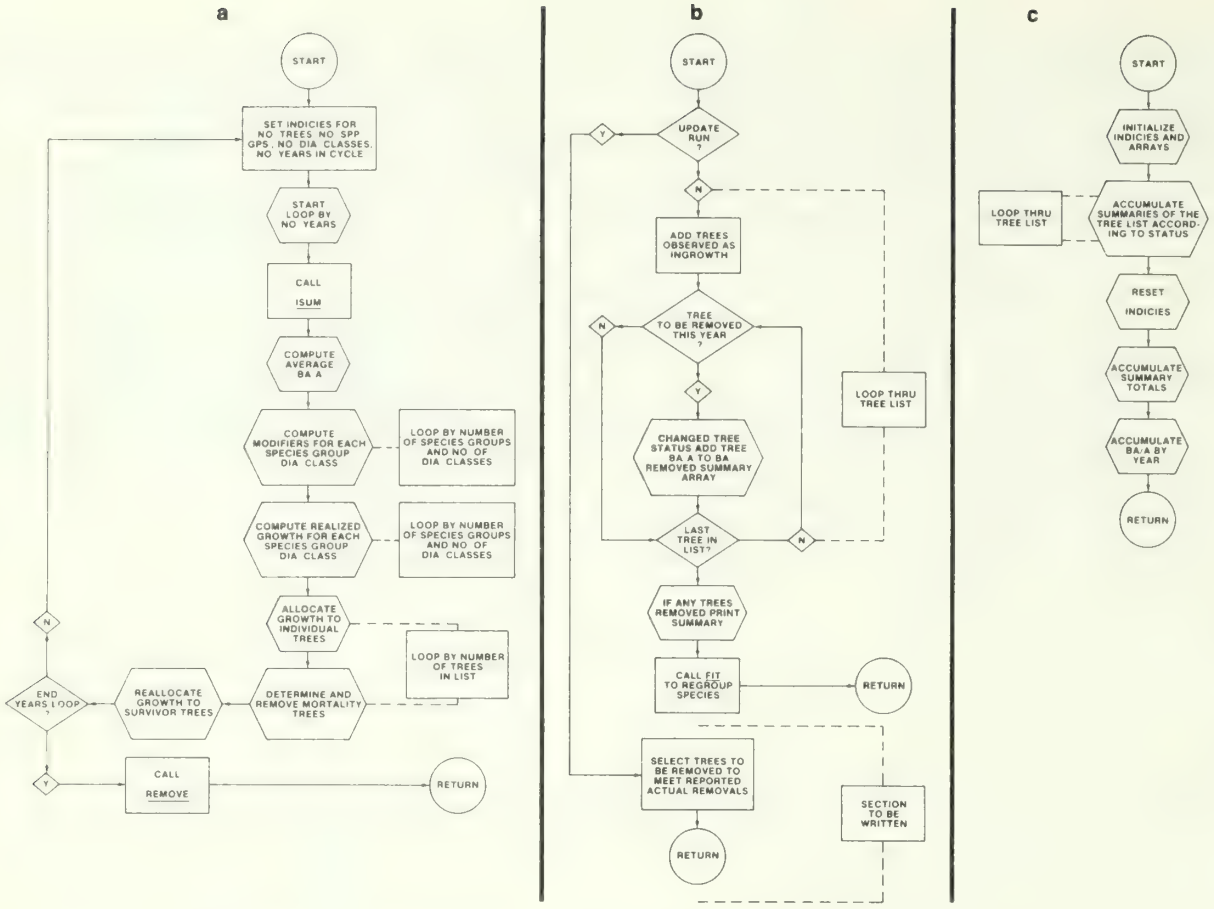

a
START
SET INDICIES FOR NO TREES NO SPP GPS, NO DIA CLASSES, NO YEARS IN CYCLE
START LOOP BY NO YEARS
CALL ISUM
COMPUTE AVERAGE BA A
COMPUTE MODIFIERS FOR EACH SPECIES GROUP DIA CLASS
LOOP BY NUMBER OF SPECIES GROUPS AND NO OF DIA CLASSES
COMPUTE REALIZED GROWTH FOR EACH SPECIES GROUP DIA CLASS
LOOP BY NUMBER OF SPECIES GROUPS AND NO OF DIA CLASSES
ALLOCATE GROWTH TO INDIVIDUAL TREES
LOOP BY NUMBER OF TREES IN LIST
N
END YEARS LOOP ?
REALLOCATE GROWTH TO SURVIVOR TREES
DETERMINE AND REMOVE MORTALITY TREES
Y
CALL REMOVE
RETURN
b
START
Y
UPDATE RUN ?
N
ADD TREES OBSERVED AS INGROWTH
N
TREE TO BE REMOVED THIS YEAR ?
Y
LOOP THRU TREE LIST
CHANGED TREE STATUS ADD TREE BA A TO BA REMOVED SUMMARY ARRAY
LAST TREE IN LIST?
N
IF ANY TREES REMOVED PRINT SUMMARY
CALL FIT TO REGROUP SPECIES
RETURN
SELECT TREES TO BE REMOVED TO MEET REPORTED ACTUAL REMOVALS
SECTION TO BE WRITTEN
RETURN
c
START
INITIALIZE INDICIES AND ARRAYS
LOOP THRU TREE LIST
ACCUMULATE SUMMARIES OF THE TREE LIST ACCORDING TO STATUS
RESET INDICIES
ACCUMULATE SUMMARY TOTALS
ACCUMULATE BA/A BY YEAR
RETURN

Figure 6.—Subroutines (a) **GROW,** *(b)* **REMOVE,** *and (c)* **ISUM.**

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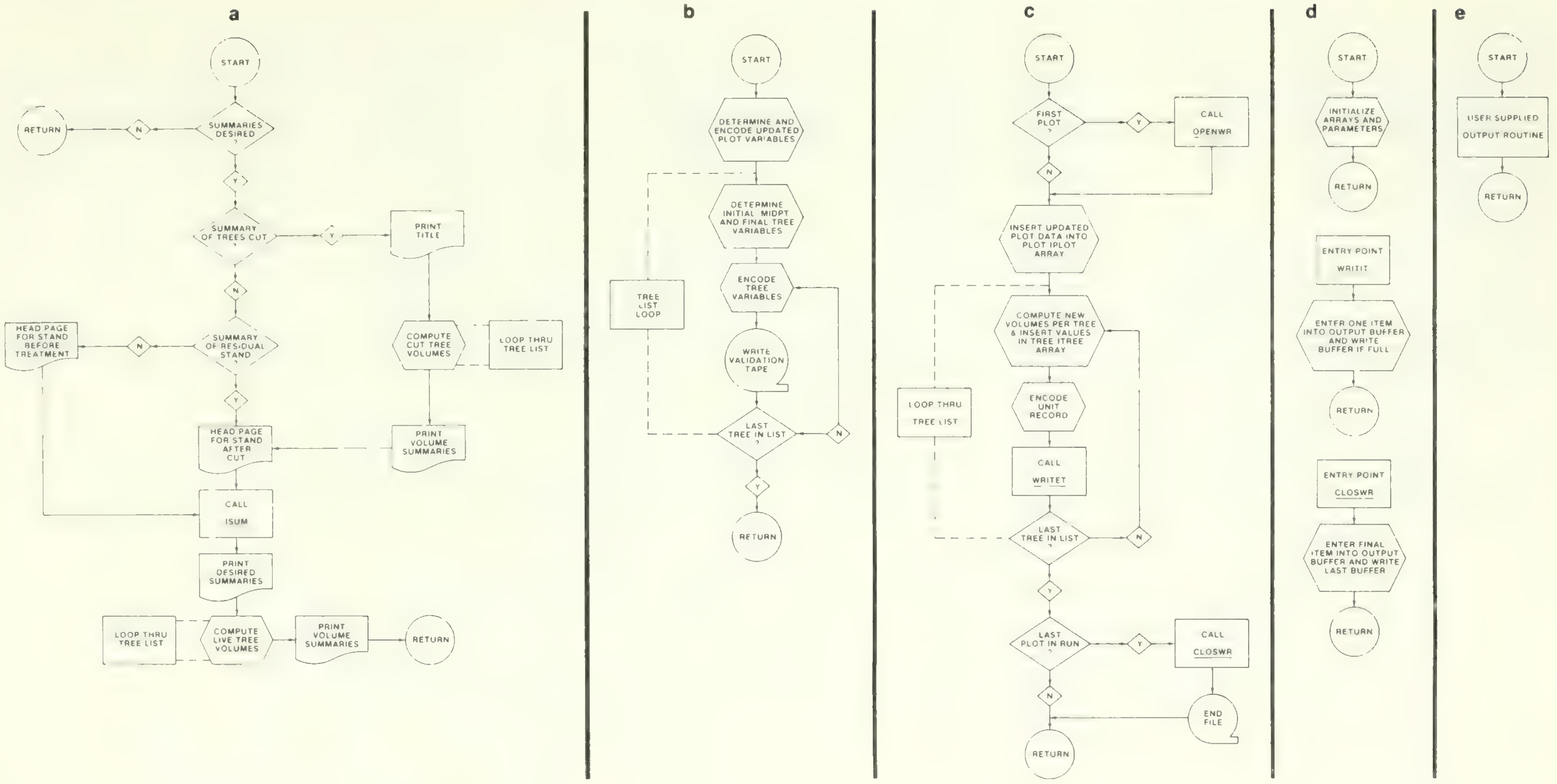

Figure 7.—Subroutines (a) **OUTPT1,** *(b)* **OUTPT2,** *(c)* **TFILE,** *(d)* **OPENWR,** *and (e)* **OUTUR.**

APPENDIX A

```
                 TEST OF UPDATE CHANGES USING CLOQUET FILE

     THIS IS A VALIDATION RUN -    1 PLOTS WILL BE PROCESSED
               ----------

     DATA WILL BE READ FROM LOGICAL UNIT 11 USING MASTER FORMAT

     OUTPUT WILL CONSIST OF PROPERTY SUMMARIES PLUS USER SPECIFIED TAPE FILE AND    VALIDATION SUMMARIES

     THE PLOT SUMMARIES CALLED FOR AND THEIR ORDER ARE-
        1    2    3    4    5    6    7

     THE PROJECTION WILL CONSIST OF   5 CYCLES OF   2 YEARS EACH

     THE RANDOM NUMBER INITIALIZATION VALUE IS 31 WHICH GIVES A SEED VALUE OF     .6778029E+00

  SPECIES GROUP ASSIGNMENTS ARE-
                     NUMBER SPECIES GROUPS = 31 CODE OTHER SOFTWOODS = 10 CODE OTHER HARDWOODS = 30
     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG     SPP.  SG
       12   5       71   7       94   4       95   6      105   1      125   2      129   3      130   1      241   8      261   9
      314  18      316  14      317  13      318  18      371  16      375  26      402  23      403  23      405  23      407  23
      409  23      541  19      543  11      544  11      741  25      742  12      743  24      746  25      802  20      804  20
      806  22      809  22      823  20      826  20      830  22      832  20      833  21      834  21      837  22      951  17
      972  15      974  15      975  15      977  15      999  31

  SPECIES GROUPS ARE-
   1 JACK PINE      2 RED PINE       3 WHITE PINE     4 WH. SPRUCE     5 BALSAM FIR     6 BLK.SPRUCE     7 TAMARACK       8 N.WH.CEDAR
   9 HEMLOCK       10 OTHER SWDS    11 BLK.GR.ASH    12 COTTONWOOD    13 SIL.MAPLE     14 RED MAPLE     15 ELM           16 YEL.BIRCH
  17 BASSWOOD      18 HARD MAPLE    19 WHITE ASH     20 WHITE OAK     21 S.RED OAK     22 O.RED OAK     23 HICKORY       24 B.T.ASPEN
  25 QUAK.ASPEN    26 PAP.BIRCH     27               28               29               30 OTHER HWDS    31 NONCOMMER.    32 TOTAL


                              PARAMETERS TO COMPUTE C.R. AS A FUNCTION OF AVERAGE BASAL AREA
S.G.  PARAMETER1  PARAMETER2  PARAMETER3  PARAMETER4  PARAMETER5      S.G.  PARAMETER1  PARAMETER2  PARAMETER3  PARAMETER4  PARAMETER5
  1       0         8.000     .1870E-01    2.000     .8490E-01         2        0         8.000     .1270E-01    2.000      .5040E-01
  3       0         8.000     .6000E-02    2.000     .1399             4        0         8.000     .5800E-02    2.000      .8150E-01
  5       0         8.000     .5800E-02    2.000     .8150E-01         6        0         8.000     .3900E-02    2.000      .1045
  7       0         8.000     .3900E-02    2.000     .1045             8        0         8.000     .2130E-01    2.000      .5500E-02
  9       0         8.000     .2130E-01    2.000     .5500E-02        10        0         8.000     .2130E-01    2.000      .5500E-02
 11       0         3.410        0           0          0             12    -.1860E-01    6.910        0           0        .4760E-01
 13   -.1860E-01    6.910        0           0       .4760E-01        14    -.1860E-01    6.910        0           0        .4760E-01
 15       0         3.040        0           0          0             16    -.2220E-01    6.019        0           0        .2640E-01
 17       0         3.000        0           0          0             18    -.6400E-02    4.707        0           0        .2820E-01
 19       0         3.410        0           0          0             20    -.8000E-02    4.728        0           0        .3810E-01
 21   -.8000E-02    4.728        0           0       .3810E-01        22    -.8000E-02    4.728        0           0        .3810E-01
 23   -.8000E-02    4.728        0           0       .3810E-01        24    -.7000E-02    4.298        0           0        .2300E-01
 25   -.7000E-02    4.298        0           0       .2300E-01        26    -.7000E-02    4.298        0           0        .2300E-01
 27   -.7000E-02    4.298        0           0       .2300E-01        28    -.7000E-02    4.298        0           0        .2300E-01
 29   -.7000E-02    4.298        0           0       .2300E-01        30    -.7000E-02    4.298        0           0        .2300E-01
 31   -.7000E-02    4.298        0           0       .2300E-01
```

```
FOREST TYPES FOR THIS RUN ARE-
   1 JACK PINE              2 RED PINE               3 WHITE PINE            11 SPRUCE-FIR            12 BLACK SPRUCE
  14 N. WHITE CEDAR        15 TAMARACK              50 OAK-HICKORY           70 LOWLAND HARDWOODS     80 NORTHERN HARDWOODS
  91 ASPEN                 92 PAPER BIRCH           90 ASPEN-BIRCH           99 NON-STOCKED           -0


                           CRITICAL VALUES FOR DECISION VARIABLES

                           VARIABLE POSITION IN SILVICULTURAL GUIDE
   TYPE         1/212/22  3/23  4/24  5/25  6/26  7/27  8/28  9/29 10/30    11    12    13    14    15    16    17    18    19    20

JACK PINE      5.0 400.020 6.0  60.0  40.0  70.0  60.0 140.0 120.0  80.0    .7  68.91141.0  40.4

RED PINE       5.0 400.0   2.0   9.0  15.0  20.02000.0 160.0 160.0 140.0 120.0 140.0 180.0 200.0  90.0    .5 120.0    .5 150.0  86.4
            1328.0  85.9

WHITE PINE     5.0 400.0  70.0  40.0 120.0  40.0  40.0  40.0  40.0  60.0     0     0     0     0 117.92934.0 147.8

SPRUCE-FIR    40.0  50.0  15.0  20.0  40.0 100.0  45.0  35.0 140.0  75.0 100.0  65.0

B. SPRUCE     25.0 147.6 571.9   3.3  80.0-175.4   2.6

SWAMP CON.    25.0  36.0 120.0  50.0  60.0  80.0  90.0 100.0  50.0  60.0  80.0  60.0  60.0

LOW. HDWD.    55.0  75.0  80.0 100.0 100.0  65.0  65.0  75.0

N. HDWD.       2.0   4.650 0.01000.0  80.0   9.6  20.0  16.0  20.0  70.0 110.0  75.0 160.0 150.0  80.0  80.0  85.0 120.0  70.0  70.0
              70.0     0  15.0  15.0

OAK-HICK.     55.0  75.0  80.0 100.0  60.0  60.0  50.0  70.0    .5    .5    .5  10.0  10.0  10.0  16.0  20.0  24.0  10.0  25.0  10.0
              25.0  10.0  25.0  15.0  15.0  15.0  47.22443.0  20.5  65.0 887.0  54.3

ASPEN         40.0  35.0  35.0  55.0  55.0  75.0 100.0  35.0  60.0  50.0  75.0  45.0  50.0  75.0  85.0 110.0  90.0   6.0  55.0  80.0
               6.0

P. BIRCH      40.0  35.0  35.0  55.0  55.0  75.0 100.0  35.0  60.0  50.0  75.0  45.0  50.0  75.0  85.0 110.0  90.0   6.0  55.0  80.0
               6.0

N.W. CEDAR    25.0  36.0 120.0  50.0  60.0 150.0  50.0  60.0 130.0 200.0 200.0 150.0  60.0 150.0  60.0

TAMARACK        -0    -0

UNDERSTKD.    20.0  10.0
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                              VOLUME REGRESSION EQUATION PARAMETERS

          NUMBER OF EQUATIONS =  6 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC FOOT VOLUME TREE CLASS 10

  SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
  EQUATION NO.   1  1  1  2  2  2  2  2  2  2  4  5  4  4  6  4  6  4  4  3  3  3  3  5  5  5  6  6  6  6  6

             EQUA.          PARA.1           PARA.2           PARA.3           PARA.4              PARA.5
               1          36048.68       .4024466E-04       1.173027        -.1517975               -0
               2          385.4175       .1070582E-03       1.350854        -.2868318               -0
               3          1317.764       .4733759E-03       1.462066        -.1206417               -0
               4          25157.29       .4449758E-04       1.177665        -.1559213               -0
               5          562.9609       .7814853E-03       1.549974        -.1390638               -0
               6          537.5624       .5394414E-03       1.295829        -.2497832               -0

          NUMBER OF EQUATIONS = 16 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC FOOT VOLUME TREE CLASS 20

  SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
  EQUATION NO.   3  2  1  4  5  4  6  6  6  6 12 12 11 11 16  9 15 10 12  7  7  8  8 13 14 13 16 16 16 16 16

             EQUA.          PARA.1           PARA.2           PARA.3           PARA.4              PARA.5
               1          1199.625       .4136829E-03       1.268860        -.2083986               -0
               2          127.1188       .3939387E-03       1.810027        -.1883882               -0
               3          63.06930       .1042520E-02       1.888101        -.2019203               -0
               4          573.3734       .4495926E-03       1.571015        -.1433549               -0
               5          591.3112       .4327938E-03       1.563568        -.1418235               -0
               6          565.4679       .4310511E-03       1.290465        -.2412149               -0
               7          777.4550       .8723104E-03       1.468083        -.1239891               -0
               8          397.7769       .1007421E-02       1.527054        -.1354224               -0
               9          118.3166       .1889391E-03       1.831568        -.1925592               -0
              10          246.6457       .4292254E-03       1.666395        -.1624640               -0
              11          714.8841       .6664804E-03       1.494599        -.1290761               -0
              12          11794.38       .9004474E-04       1.183965        -.1608640               -0
              13          144.3193       .1482680E-02       1.710300        -.1696353               -0
              14          64.81606       .1126818E-02       1.897307        -.2034324               -0
              15          773.7419       .5591250E-03       1.505967        -.1306789               -0
              16          559.6307       .6039853E-03       1.288580        -.2364948               -0

          NUMBER OF EQUATIONS =  6 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC FOOT VOLUME TREE CLASS 30

  SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
  EQUATION NO.   1  1  1  2  2  2  2  2  2  2  4  5  4  4  6  4  6  4  4  3  3  3  3  5  5  5  6  6  6  6  6

             EQUA.          PARA.1           PARA.2           PARA.3           PARA.4              PARA.5
               1          627.0185       .3466743E-03       1.498787        -.1265395               -0
               2          10276.78       .2696920E-04       1.206486        -.1784514               -0
               3          114.7355       .9698185E-03       1.702548        -.1870065               -0
               4          265.0794       .1087531E-02       1.623151        -.1333784               -0
               5          3011.090       .9405998E-04       1.446883        -.1156433               -0
               6          101425.5       .3047962E-05       1.383356        -.7984840E-01           -0
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                                    VOLUME REGRESSION EQUATION PARAMETERS

              NUMBER OF EQUATIONS =  5 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC FOOT VOLUME TREE CLASS 40

     SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
     EQUATION NO.   1  1  1  1  1  1  1  1  1  1  3  4  3  3  5  3  5  3  3  2  2  2  2  4  4  4  5  5  5  5  5

            EQUA.        PARA.1          PARA.2           PARA.3           PARA.4              PARA.5
              1        812.3681     .4154177E-04       1.478718       -.1223292                  -0
              2        133.2531     .5246846E-01       1.252944       -.2518464E-01              -0
              3        47.71806     .3359426E-02       1.962034       -.1313597                  -0
              4        4846.439     .4103629E-04       1.390071       -.1031025                  -0
              5        329.7758     .4718038E-02       1.364578       -.9341189E-01              -0

              NUMBER OF EQUATIONS =  6 FOR WISCONSIN NORTHEASTERN UNIT 1  BOARD FOOT VOLUME TREE CLASS 10

     SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
     EQUATION NO.   1  1  1  2  2  2  2  2  2  2  4  5  4  4  6  4  6  4  4  3  3  3  3  5  5  5  6  6  6  6  6

            EQUA.        PARA.1          PARA.2           PARA.3           PARA.4              PARA.5
              1        257231.5     .2784675E-04       1.171308       -.1504486                  -0
              2        5683.337     .3319345E-03       1.275705       -.2313738                  -0
              3        42344.65     .1357544E-03       1.197160       -.1710607                  -0
              4        106680.1     .5604898E-04       1.182841       -.1596589                  -0
              5        11165.41     .3651559E-03       1.237404       -.2041724                  -0
              6        3083.508     .5270820E-03       1.293385       -.2494871                  -0

              NUMBER OF EQUATIONS = 13 FOR WISCONSIN NORTHEASTERN UNIT 1  BOARD FOOT VOLUME TREE CLASS 20

     SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
     EQUATION NO.   3  2  1  4  5  4  7  7  6  7 11 12 11 11 13  9 13 10 11  8  8  8  8 12 12 12 13 13 13 13 13

            EQUA.        PARA.1          PARA.2           PARA.3           PARA.4              PARA.5
              1        11183.54     .2437308E-03       1.242120       -.2037176                  -0
              2        4302.868     .1037676E-02       1.253822       -.2153252                  -0
              3        13971.63     .2434394E-03       1.217312       -.1889183                  -0
              4        769248.0     .4628491E-05       1.170987       -.1501769                  -0
              5        527215.0     .6197405E-05       1.173399       -.1522792                  -0
              6        6558.332     .3089813E-03       1.256708       -.2172892                  -0
              7        895.7112     .3537490E-03       1.363223       -.2990378                  -0
              8        17587.02     .5285970E-03       1.185383       -.1617882                  -0
              9        1352.299     .5313031E-03       1.677255       -.1443074                  -0
             10        1438.785     .2009731E-03       1.347552       -.2837179                  -0
             11        851.1028     .3350519E-02       1.321802       -.2657067                  -0
             12        4977.429     .4298018E-03       1.260356       -.2211002                  -0
             13        3921.671     .6729626E-03       1.264172       -.2211569                  -0

              NUMBER OF EQUATIONS =  2 FOR WISCONSIN NORTHEASTERN UNIT 1  BOARD FOOT VOLUME TREE CLASS 31

     SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
     EQUATION NO.   1  1  1  1  1  1  1  1  1  1  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2

            EQUA.        PARA.1          PARA.2           PARA.3           PARA.4              PARA.5
              1        730020.7     .7777858E-05       1.111671       -.1306388                  -0
              2        528516.2     .2979013E-04       1.090030       -.9087071E-01              -0
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                              VOLUME REGRESSION EQUATION PARAMETERS

          NUMBE  OF EQUATIONS =  6 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC VOLUME IN SAWLOG PORTION T.C. 10

SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
EQUATION NO.   1  1  1  2  2  2  2  2  2  2  4  5  4  4  6  4  6  4  4  3  3  3  3  5  5  5  6  6  6  6  6

          EQU.         PARA.1           PARA.2          PARA.3          PARA.4          PARA.5
            1        3464.167       .2459303E-03      1.216782       -.1865286         -0
            2         400.2449      .1091619E-03      1.485718       -.2090047         -0
            3       12966.89        .9830624E-04      1.181643       -.1592031         -0
            4       15909.84        .9668812E-04      1.175707       -.1542967         -0
            5        2546.492       .3029995E-03      1.227451       -.1948611         -0
            6         407.4863      .5449546E-03      1.310683       -.2574237         -0

          NUMBE  OF EQUATIONS = 13 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC VOLUME IN SAWLOG PORTION T.C. 20

SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
EQUATION NO.   3  2  1  4  5  4  7  7  6  7 11 12 11 11 13  9 13 10 11  8  8  8  8 12 12 12 13 13 13 13 13

          EQU.         PARA.1           PARA.2          PARA.3          PARA.4          PARA.5
            1        1376.083       .4558337E-03      1.242193       -.2061520         -0
            2        3477.933       .5337996E-03      1.191640       -.1672472         -0
            3         760.2680      .5237971E-03      1.258388       -.2185038         -0
            4        9547.071       .4612539E-04      1.210569       -.1816787         -0
            5        8077.398       .3716047E-04      1.221318       -.1900312         -0
            6         961.1018      .6550633E-03      1.248353       -.2110187         -0
            7        1956.803       .2003224E-03      1.235392       -.2009995         -0
           11        2341.854       .7628486E-03      1.194051       -.1691050         -0
           12         686.4042      .5122937E-03      1.269858       -.2279520         -0
           13        1239.743       .7069922E-03      1.231405       -.1980232         -0

          NUMBE  OF EQUATIONS =  2 FOR WISCONSIN NORTHEASTERN UNIT 1  CUBIC VOLUME IN SAWLOG PORTION T.C. 31

SPECIES GROUP  1  2  3  4  5  6  7  8  9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31
EQUATION NO.   1  1  1  1  1  1  1  1  1  1  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2  2

          EQU.         PARA.1           PARA.2          PARA.3          PARA.4          PARA.5
            1        3160.909       .5497128E-04      1.232636       -.1987996         -0
            2         122.0531      .9674253E-04      1.480889       -.2655163         -0
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                                     MORTALITY EQUATION ASSIGNMENTS AND PARAMETERS
SPECIES GP   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26  27  28  29  30  31
  EQUATION   1   2   3   4   5   6   7   8   9   2  10  11  11  11  12  13  14  15  16  17  18  19  20  21  22  23  24  24  24  24  25
         EQ.NO.      PARAMETER1          PARAMETER2          PARAMETER3          PARAMETER4          PARAMETER5
              1      .3676700            60.17800            1.072700            .5020000E-02        .1222000
              2      1.084300            11.01200            .5886600            .2000000E-03        .4850000
              3      2.350700            33.60900            1.008800            .2010000E-02               0
              4      2.880600            30.77400            1.230900            .3960000E-02               0
              5      2.697600            30.55000            .8996300            .4000000E-02       -.2306900
              6      2.877400            432.9500            1.857600            .2350000E-02               0
              7      .3676700            60.17800            1.072700            .5020000E-02        .1222000
              8      2.877400            432.9500            1.857600            .2350000E-02               0
              9      2.823300            89.56000            1.096600            .3200000E-02               0
             10      1.487500            13.33800            .5429000            .1800000E-03               0
             11      2.240500            56.59400            1.039200            .4940000E-02               0
             12      1.988900            44.54100            1.096500            .8990000E-02               0
             13      2.670500            63.14800            1.381900            .3820000E-02               0
             14      -.5861200           101.8700            1.649300            .4890000E-02        .6839800
             15      .8150000            66.93700            1.593400            .4350000E-02        .7500000
             16      1.782100            232.3100            1.726700            .2220000E-02               0
             17      3.694600            95.63700            1.491700            .1880000E-02               0
             18      2.309200            6999.800            2.661500            .4680000E-02               0
             19      -1.149200           9.108700            2.455200                   0            .3500000
             20      3.062600            63.49500            1.049800            .1340000E-02               0
             21      .8805000            56.59300            1.215400            .1288000E-01               0
             22      -.7855000E-01       213.6300            1.712600            .2276000E-01        .2581200
             23      2.180800            11.62600            .4750000            .2900000E-03               0
             24      2.233900            29.62900            1.342700            .7480000E-02               0
             25      2.358100            113.0600            .9993000            .1923000E-01               0


                                  POTENTIAL GROWTH EQUATION ASSIGNMENTS AND PARAMETERS
SPECIES GP   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26  27  28  29  30  31
  EQUATION   1   2   3   4   5   6   7   8   9   1  10  11  11  11  12  13  14  15  16  17  18  19  20  21  22  23  24  24  24  24  24
         EQ.NO.      PARAMETER1          PARAMETER2          PARAMETER3          PARAMETER4          PARAMETER5
              1      .1606200            -.9000000E-05       3.624500            .4000000E-04        1.000000
              2      .9446000E-01        -.1200000E-03       2.059600            .3500000E-03        .2422500
              3      .2557800            -.8800000E-03       1.726300            .4000000E-04        1.000000
              4      .1705600            -.1451600E-01       1.066000            .5200000E-03        .2729800
              5      .1220000            -.6000000E-03       1.989000            .6000000E-04        1.000000
              6      .1071300            -.1070000E-02       2.001700            .6000000E-04        .9112700
              7      .1114700            -.1000000E-04       3.068500            .3000000E-04        1.000000
              8      .1340300            -.1000000E-05       3.688000            .2000000E-04        1.000000
              9      .1687200            -.3000000E-06       3.573800            .1000000E-04        1.000000
             10      .5880700E-01        -.6000000E-08       5.055900            .2400000E-03        .3155300
             11      .1094800            -.4000000E-04       2.222600            .5000000E-03        .6626000E-01
             12      .2849600            -.1820000E-02       1.529700            .3000000E-04        1.000000
             13      .1515500            -.3000000E-05       3.310400            .7000000E-04        .5730200
             14      .2540200            -.4000000E-05       2.939600            .1000000E-04        1.000000
             15      .1877200            -.7000000E-05       2.583900            .2800000E-03        .8385000E-01
             16      .2116700            -.3000000E-05       3.313100            .1000000E-04        .1243000
             17      .1265400            -.4000000E-05       2.753800            .5000000E-04        .6208600
             18      .1553500            -.1000000E-06       3.536700            .1800000E-03        .2590000
             19      .1735800            -.7000000E-04       2.445100            .3000000E-04        .9522200
             20      .1647100            -.2161000E-02       1.394900            .4000000E-04        .7162800
             21      .2349000            -.9420000E-02       1.104100            .3600000E-03        .1538600
             22      .2164500            -.9100000E-04       2.603000            .4400000E-04        1.000000
             23      .1097100            -.3200000E-03       2.023600            .3400000E-03        .2128800
             24      .3751000            -.2479000E-01       .9628800            .4000000E-04        1.000000
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FIRST PARAMETER OF BETA FUNCTION AND SPECIES INTERACTION ARRAY

SPECIES GROUP	SPECIES GROUP 1,12,23	2,13,24	3,14,25	4,15,26	5,16,27	6,17,28	7,18,29	8,19,30	9,20,31	10,21	11,22
1	-112.0	.4830	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.355	1.000	1.000	1.000	1.000	1.000	1.000		
2	2.757	-121.6	1.192	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	2.261	3.545	1.000	1.000	1.000	1.000	1.000		
3	1.000	1.098	-117.4	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.432	.2860	1.000
	1.000	1.000	.6620	1.000	1.000	1.000	1.000	1.000	1.000		
4	1.000	1.000	1.000	-124.6	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
5	1.000	1.000	1.000	1.000	-86.29	1.000	1.000	.2860	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	2.327	1.000	1.000	1.000	1.000	1.000	1.000		
6	1.000	1.000	1.000	1.000	1.000	-124.6	3.523	3.066	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	.2860	1.000	1.000	1.000	1.000	1.000	1.000		
7	1.000	1.000	1.000	1.000	1.000	.2840	-52.34	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
8	1.000	1.000	1.000	1.000	3.500	.3630	1.000	-155.5	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
9	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-117.4	1.000	1.000
	1.000	1.000	1.000	1.000	.4570	1.000	.9770	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
10	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-117.4	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
11	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	-73.59
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
12	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	-68.80	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
13	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	-68.80	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
14	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	-68.80	1.000	1.205	1.000	1.186	1.000	1.000	.5890	1.000
	1.000	1.000	.5740	2.677	1.000	1.000	1.000	1.000	1.000		
15	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	-73.59	1.000	2.010	.8240	1.000	.2930	.6040	1.000
	1.000	1.000	1.441	1.000	1.000	1.000	1.000	1.000	1.000		
16	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	2.189	1.000	1.000
	1.000	1.000	.8590	1.000	-72.83	1.000	1.330	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		
17	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	.7000	1.000	-72.83	1.317	1.000	1.000	1.000	1.000
	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000		

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 18  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.598   1.000   1.000
     1.000   1.000   1.571   1.431   .7500   .9760  -73.59   .9650   1.000   .6480   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 19  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.589  -73.59   1.000   2.346   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 20  1.000   1.000   .7760   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   3.414   1.000   1.000   1.000   1.000  -72.83   1.601   3.546
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 21  1.000   1.000   3.500   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   2.321   2.090   1.000   1.000   2.357   .4270   .9770  -72.83   .8930
     1.000   2.497   2.324   1.000   1.000   1.000   1.000   1.000   1.000

 22  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   .2820   1.120  -72.83
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 23  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
    -72.83   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 24  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   .4470   1.000
     1.000  -117.4   1.000   1.000   1.000   1.000   1.000   1.000   1.000

 25  .8290   .4550   1.783   1.000   .5810   3.500   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.829   .8800   1.000   1.000   1.000   1.000   1.000   .4990   1.000
     1.000   1.000  -116.9   3.500   1.000   1.000   1.000   1.000   1.000

 26  1.000   .2820   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   .3890   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   .2860  -117.4   1.000   1.000   1.000   1.000   1.000

 27  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000  -72.83   1.000   1.000   1.000   1.000

 28  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000  -72.83   1.000   1.000   1.000

 29  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000  -72.83   1.000   1.000

 30  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000  -72.83   1.000

 31  1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000
     1.000   1.000   1.000   1.000   1.000   1.000   1.000   1.000  -72.83


                         SECOND AND THIRD PARAMETERS FOR BETA FUNCTION
                                         SPECIES GROUP
PARAM 1,12,23  2,13,24  3,14,25  4,15,26  5,16,27  6,17,28  7,18,29  8,19,30  9,20,31   10,21    11,22

  2  -.4638   -.4462   -.1261   -.3652   -.4923   -.3652   -.4441   -.2230   -.1261   -.1261   -.1902
     -.1434   -.1434   -.1434   -.1902   -.1303   -.1303   -.1902   -.1902   -.1303   -.1303   -.1303
     -.1303   -.1261   -.1366   -.1261   -.1303   -.1303   -.1303   -.1303   -.1303

  3  1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000
     1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000
     1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000    1.000
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                                         ALLOCATION RULE EQUATION ASSIGNMENT AND PARAMETERS
                        PARAMETERS 1-3 ARE USED TO DETERMINE THE VALUE OF -A- AND PARAMETERS 4-7 FOR THE VALUE OF -B-
SPECIES GP   1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26  27  28  29  30  31
  EQUATION   1   3   5   7   9  11  11  13   3   1  19  19  19  19  19  19  19  15  19  19  19  19  19  17  17  17  19  19  19  19  19

          EQUA.      PARA.1        PARA.2        PARA.3        PARA.4        PARA.5        PARA.6        PARA.7
            1     -.6295E-01    -.7303E-03     .7711E-05     .1000E+00    -.4000E-02     .1500E+03     .7400E+00
            2     -.6295E-01    -.7303E-03     .7711E-05     .1000E+00    -.4000E-02     .1500E+03     .7400E+00
            3     -.6431E-01    -.9678E-03     .5162E-05     .2000E+00    -.9447E-02     .3000E+03     .4102E+01
            4     -.8437E-01    -.5417E-03     .3802E-05     .1500E+00    -.5585E-02     .3000E+03     .2139E+01
            5     -.7361E-01    -.3537E-03     .1422E-05     .1000E+00    -.7298E-03     .2500E+03     .1759E+00
            6     -.7361E-01    -.3537E-03     .1422E-05     .1000E+00    -.7298E-03     .2500E+03     .1759E+00
            7     -.1111E+00    -.1006E-03     .3391E-05     .1000E+00    -.1799E-01     .2500E+03     .8264E+01
            8     -.1111E+00    -.1006E-03     .3391E-05     .1000E+00    -.1799E-01     .2500E+03     .8264E+01
            9     -.8707E-01    -.2422E-03     .2826E-05     .1000E+00    -.1720E-02     .2500E+03     .3479E+00
           10     -.8707E-01    -.2422E-03     .2826E-05     .1000E+00    -.1720E-02     .2500E+03     .3479E+00
           11     -.1101E+00     .6208E-04    -.7802E-07     .1000E+00    -.3190E-02     .2500E+03     .3756E+00
           12     -.1101E+00     .6208E-04    -.7802E-07     .1000E+00    -.3190E-02     .2500E+03     .3756E+00
           13     -.1536E+00     .5834E-03    -.1198E-05     .1000E+00    -.2018E-02     .4000E+03     .3724E+00
           14     -.1536E+00     .5834E-03    -.1198E-05     .1000E+00    -.2018E-02     .4000E+03     .3724E+00
           15     -.8396E-01    -.2447E-03     .2451E-05     .1000E+00    -.6177E-02     .2500E+03     .8322E+00
           16     -.8396E-01    -.2447E-03     .2451E-05     .1000E+00    -.6177E-02     .2500E+03     .8322E+00
           17     -.8195E-01    -.2475E-03     .2478E-05     .1000E+00    -.3471E-02     .2500E+03     .7540E+00
           18     -.8195E-01    -.2475E-03     .2478E-05     .1000E+00    -.3471E-02     .2500E+03     .7540E+00
           19     -.3939E-01    -.1959E-02     .1513E-04     .1000E+00    -.2297E-01     .2000E+03     .6384E+01
           20     -.3939E-01    -.1959E-02     .1513E-04     .1000E+00    -.2297E-01     .2000E+03     .6384E+01


                                              SPECIES ASSIGNMENT PRIORITY ARRAY
         1   2   3   4   5   6   7   8   9  10  11  12  13  14  15  16  17  18  19  20  21  22  23  24  25  26  27  28  29  30  31
     1  -1   8  18  11   3   1   2   4  19  25   6  23  24  16  17  20  14  13  15  21  22   9   5  10  12   7   0   0   0  26  27
     2  21  -1  15   5   2  22   8   1  16  23   9  24  25  13  14  17  11  10  12  18  19   3  20   4   7   6   0   0   0  26  27
     3  21  14  -1  11  16  22  18  15   2  23  19  24  25   3   1   4   7   9   5   6   8  13  20  12  10  17   0   0   0  26  27
     4  20   6  13  -1  10  22  14   8  15  23  16  24  25   9  11  17   5   3   7  19  21   4  18   2   1  12   0   0   0  26  27
     5   5   2  18   4  -1   6   3   1  19  23   9  24  25  16  17  20  14  13  15  21  22   8  12  10  11   7   0   0   0  26  27
     6   1   5  18   9   3  -1   2   4  19  23   7  24  25  16  17  20  14  13  15  21  22  10   6  11  12   8   0   0   0  26  27
     7   2   5  18   6   1   4  -1   3  19  23   8  24  25  16  17  20  14  13  15  21  22  10   9  11  12   7   0   0   0  26  27
     8   5   1  18   3   2   6   4  -1  19  23   8  24  25  16  17  20  14  13  15  21  22   9  10  11  12   7   0   0   0  26  27
     9  21  14   1  11  16  22  18  15  -1  23  19  24  25   6   3   2   8   9   7   4   5  13  20  12  10  17   0   0   0  26  27
    10   1   9  19  12   4   2   3   5  26  -1   7  24  25  17  18  21  15  14  16  22  23  10   6  11  13   8   0   0   0  26  27
    11  11  15  19  16  12  13   9  14  20  27  -1  24  25   8  18  21   6   5   7  22  23   2  10   3   4   1   0   0   0  26  27
    12  24  17  14  16  19  25  21  18  15  27  22  -1   2   1   4  11   5   6   3  12  13  10  23   9   8  20   0   0   0   7  26
    13  24  17  14  16  19  25  21  18  15  27  22   2  -1   1   4  11   5   6   3  12  13  10  23   9   8  20   0   0   0   7  26
    14  24  17  14  16  19  25  21  18  15  27  22  13  12  -1   2   9   3   4   1  10  11   8  23   7   6  20   0   0   0   5  26
    15  24  17  14  16  19  25  21  18  15  26  22  12  13   2  -1   4   5   7   3   6   8  11  23  10   9  20   0   0   0   1  27
    16  24  17  14  16  19  25  21  18  14  26  22   6   7   5   3  -1   9  10   8   1   2  13  23  12  11  20   0   0   0   4  27
    17  24  16  15  14  19  25  21  18  17  26  22  12  13   4   6   9  -1   1   2  10  11   8  23   7   3  20   0   0   0   5  27
    18  24  16  15  14  19  25  21  18  17  26  22  12  13   4   6   9   1  -1   2  10  11   8  23   7   3  20   0   0   0   5  27
    19  24  16  15  14  19  25  21  18  17  26  22  12  13   2   6   9   1   3  -1  10  11   8  23   7   5  20   0   0   0   4  27
    20  24  17  15  16  19  25  21  18  14  26  22  12  13   5   3   2   7   8   6  -1   1  11  23  10   9  20   0   0   0   4  27
    21  24  17  15  16  19  25  21  18  14  26  22  12  13   5   3   2   7   8   6   1  -1  11  23  10   9  20   0   0   0   4  27
    22  19  14  21  15  17  26  18  16  22  26   7   9  10   8  10  23   5   3   6  24  25  -1  11   1   2   4   0   0   0  12  27
    23  11  15  19  16  12  13  10  14  20  27   1  24  25   9  18  21   7   6   8  22  23   3  -1   4   5   2   0   0   0  17  26
    24  19  14  21  15  17  20  18  16  22  26   7   9  10   8  13  23   5   3   6  24  25   1  11  -1   2   4   0   0   0  12  27
    25  24  18  21  17  20  25  23  19  22  26  10  15  16   6   8  11   3   1   5  12  14   4  13   2  -1   9   0   0   0   7  27
    26  18  17  21  20  19  19  15  16  22  26   1  13  14   9  12  23   7   6   8  24  25   3   2   4   5  -1   0   0   0  11  27
    27   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
    28   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
    29   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0
    30  24  17  14  16  19  25  21  18  15  26  22  12  13   1   2   6   4   5   3   8   9  11  23  10   7  20   0   0   0  -1  27
    31   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0   0  -1
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APPENDIX B

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                                 TEST OF UPDATE CHANGES USING CLOQUET FILE
 ******** PLOT SUMMARIES AT THE END OF 1959 PLOT IDENT.      1   ********

     NUMBER OF MORTALITY TREES PER ACRE
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE              0         0
         PAP.BIRCH              0         0
         BLK.SPRUCE             0         0
         TOTAL                  0         0

     DIAMETER SUMS PER ACRE
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE          372.4     372.4
         PAP.BIRCH          125.3     125.3
         BLK.SPRUCE             0         0
         TOTAL              497.7     497.7

     BASAL AREA OF MORTALITY TREES PER ACRE
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE              0         0
         PAP.BIRCH              0         0
         BLK.SPRUCE             0         0
         TOTAL                  0         0

     BASAL AREA ON PLOT
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE            3.1       3.1
         PAP.BIRCH             .6        .6
         BLK.SPRUCE             0         0
         TOTAL                3.7       3.7

     NUMBER OF TREES PER ACRE
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE           35.0      35.0
         PAP.BIRCH           21.0      21.0
         BLK.SPRUCE             0         0
         TOTAL               56.0      56.0

     BASAL AREA PER ACRE
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE           22.0      22.0
         PAP.BIRCH            4.1       4.1
         BLK.SPRUCE             0         0
         TOTAL               26.0      26.0

     NUMBER OF TREES ON PLOT
          SPECIES                         DIAMETER CLASS
           GROUP              ALL     TOTAL
         JACK PINE            5.0       5.0
         PAP.BIRCH            3.0       3.0
         BLK.SPRUCE             0         0
         TOTAL                8.0       8.0

                     PRESENT STAND VOLUMES
             SPP.GP.    CUFT/A.   CORDS/A.    BDFT/A.
           JACK PINE     389.50       4.93    1860.35
           PAP.BIRCH      68.91        .87          0
           TOTAL         458.41       5.80    1860.35
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                                                SUMMARY STATISTICS

                                                                               INIT. LIVE TREES  15                 INIT. BA   26
PLOT    1          FOREST  YPE    1          SI   61         AGE   41          FINAL LIVE TREES  13                 FINAL BA    0
*************************************************************************************************************************************
         DBH    BA EXP T  EXP TREE  TREE        CUR.   DBH    DBH    DBH    DBH    DBH    DBH    CUT/    CUT/   TR  PRJ PRJ M1  M2  ST
TR.  TREE  PRED  FACTOR F CTOR CR    CR    TR  YEAR    OBS    OBS    PRED   OBS    PRED   OBS    DEAD    DEAD STAT SPP DBH ST  ST  OBS TR
NUM  SPP.  1976  /ACRE  / CRE INIT  CUR.   CC GROWTH  INIT   MID 1  MID 1  MID 2  MID 2  FINAL  YR OBS  YR PRD CUR GRP  CL O-P O-P FNL CL
                                                      1959   1964   1964   1969   1969
*************************************************************************************************************************************
      1     2    16     13    5     3     4     6      7      8      11      9     12     10     14      15    1   2   3   4   5   6  7
*************************************************************************************************************************************
  1  105 13.81   7.28  7.00  6.43  5.40   2   .22   9.80  11.00  11.05  11.90  12.17  12.90      0       0    1   1   1  11  11   1 20
  2  375  7.37   2.07  7.00  5.09  5.04   3   .19   6.00   7.20   6.99   8.40   7.37   9.70      0    1967    3   2   1  11  13   1 20
  3  105 17.89  12.22  7.00  6.40  5.36   2   .27  12.80  14.00  14.38  14.70  15.84  16.30      0       0    1   1   1  11  11   1 20
  4  105 13.35   6.81  7.00  7.42  6.38   2   .21   9.50  10.30  10.70  11.10  11.78  12.70      0       0    1   1   1  11  11   1 20
  5  105 16.37  10.23  7.00  4.80  3.77   3   .26  11.60  12.80  13.08  13.70  14.44      0   1972       0    1   1   1  11  11   3 20
  6  105 13.36   6.82  7.00  6.47  5.44   2   .21   9.50  10.70  10.70  11.70  11.78  12.10      0       0    1   1   1  11  11   1 20
  7  375  9.06   3.13  7.00  6.12  5.91   3   .17   5.90   6.90   6.88   7.80   7.81   9.00      0       0    1   2   1  11  11   1 20
  8  375  9.18   3.22  7.00  5.11  4.90   3   .17   6.00   7.00   6.99   8.00   7.93   9.30      0       0    1   2   1  11  11   1 20
  9   95  7.35   2.06  7.00  8.19  8.36   3   .17      0   5.30      0   6.00   6.16   6.70      0       0    1   3   1  40  11   1 20
 10  375  6.95   1.84  7.00  5.99  5.90   2   .14      0   5.20      0   6.30   5.93   7.10      0       0    1   2   1  40  11   1 20
 11   95  6.66   1.69  7.00  8.15  8.34   2   .18      0   5.60      0   6.50   6.48   7.20      0    1971    3   3   1  40  11   1 20
 12   95  7.81   2.33  7.00  7.99  7.83   2   .17      0   5.70      0   6.90   6.58   7.90      0       0    1   3   1  40  11   1 20
 13  105  6.24   1.49  7.00  3.79  3.40   3   .00      0      0      0   6.10      0   6.80      0       0    1   1   1   0  40   1 20
 14  375  6.92   1.83  7.00  5.89  5.87   3   .14      0      0      0   5.90      0   7.50      0       0    1   2   1   0  40   1 20
 15  375  6.08   1.41  7.00  4.96  4.95   4   .12      0      0      0   5.20      0   5.80      0       0    1   2   1   0  40   1 20

                                               BASAL AREA PER ACRE BY YEAR
   NUMBER OF YEARS IN RU  = 17
     26.00   27.45   28.90   30.37   31.66   33.36   39.69   41.49   41.12   42.84   44.57   50.43   50.73   52.73   54.73   56.71
     58.69   60.65

    LISTING OF IP ARRAY
         1        2        3        4        5        6        7        8        9        10

         1        3        3       15        1        3        1        1        0         2

         5        1       26       59       64       69        1        1       61        41

        37       48        0        0        0        0        0        0        0         0

        59       64       69       76
       PLOT       1 CONSISTING OF   15 TREES COMPLETED      1      1


         1 PLOTS WITH       15 TREES FROM TEST OF UPDATE CHANGES USING CLOQUET FILE
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TESTS

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The purposes of this paper are (1) to report on tests of the design for assembling projection system parts, and (2) to report on tests of projection system reliability in various use domains. The use domains are many. For example, the forest type domain covers all Lake States types; we are interested in the projection system reliability for each type. Another domain is that of stand origin mode —plantation or natural. A third relates to geographical regions within the Lake States; does the system work better in one State than in others? For which types in which State? A fourth and particularly important domain is time. What is the time decay rate for projection system reliability? Other domains include stocking levels, sites, ages, species, sample plot types (fixed or variable radius) and mean stand diameters. Each domain or combination of domains warrants investigation. In this paper we report on item 1 above and the domains of (1) cover type, (2) geographical area, (3) time, and (4) sample plot type.

TESTING MODELS OF SYSTEM DYNAMICS

Mathematicians recognize two possible sources of error in predicting the future state of a dynamic system, such as a forest stand:

(1) errors in estimating the initial state (initial conditions) of the system, and
(2) errors in the mathematical model that characterizes system dynamics.

Errors in predicted future states may be caused by either of these sources or both may act in concert. Source (2) may be further broken down into:

(a) the mathematical equations are inappropriate for describing the process,
(b) the manner of combining the equations is incorrect, and
(c) the numerical constants obtained from calibration are not those governing the system.

An example of error type 1 for the projection system is when a person does not have an observed tree list but only a dot tally of trees on the plot by, say, 4-inch diameter classes.

An example of error type 2a is if the potential of trees to grow in diameter at breast height is not satisfactorily characterized by our potential function (Hahn and Leary 1979). Error type 2b is exemplified by a finding that the realized stand growth cannot be characterized by a product of a potential and modifier functions. Error type 2c is obvious; the numerical constants in use do not characterize the specific process under test.

Considerable effort has gone into developing theoretically sound mathematical equations for describing the process of forest growth. Hence error type 2a will not be evaluated in this paper. Such evaluations belong more properly in the separate papers decribing each equation. We will, however, evaluate the projection system to assess the magnitude of type 2b and 2c errors. We are not concerned with assessing type 1 errors—this is an inventory problem. We have prevented type 1 errors by using only permanent growth plot information. To assess type 2b errors we have used the permanent growth plot information available to calibrate the mathematical equations (Christensen *et al.* 1979). If the projection system performs well when checked against the calibration data base, it may be tested against an independent data base (i.e., one not used in calibration). By doing so, and by comparing predicted future states with observed future states (starting from a known past condition) we are able to assess the magnitude of type 2c errors. The validation data base for this comes from five sources:

(1) Cloquet Experimental Forest of the College of Forestry,[1] University of Minnesota;
(2) Chequamegon National Forest, Wisconsin;
(3) Nicolet National Forest, Wisconsin;
(4) A second-growth northern hardwood study (NH-2) on an experimental forest near Marquette, Michigan; and
(5) Hiawatha National Forest, Upper Michigan.

Figure 1 shows the geographical locations of sources. The fifth source, the Hiawatha National Forest, has an eastern and a western part. The distribution of plots by age class and site index class is shown in table 1.

METHODS AND PROCEDURES

To test both the method of assembling system parts and the applicability of the system to other Lake States forest conditions, the validation option was selected in the computer program that implements the projection system (Hahn and Brand 1979). Selecting this option causes the program to:

(1) read up to four sets of observed diameter measurements for each tree on a plot and store them for comparison with sets of predicted diameters,

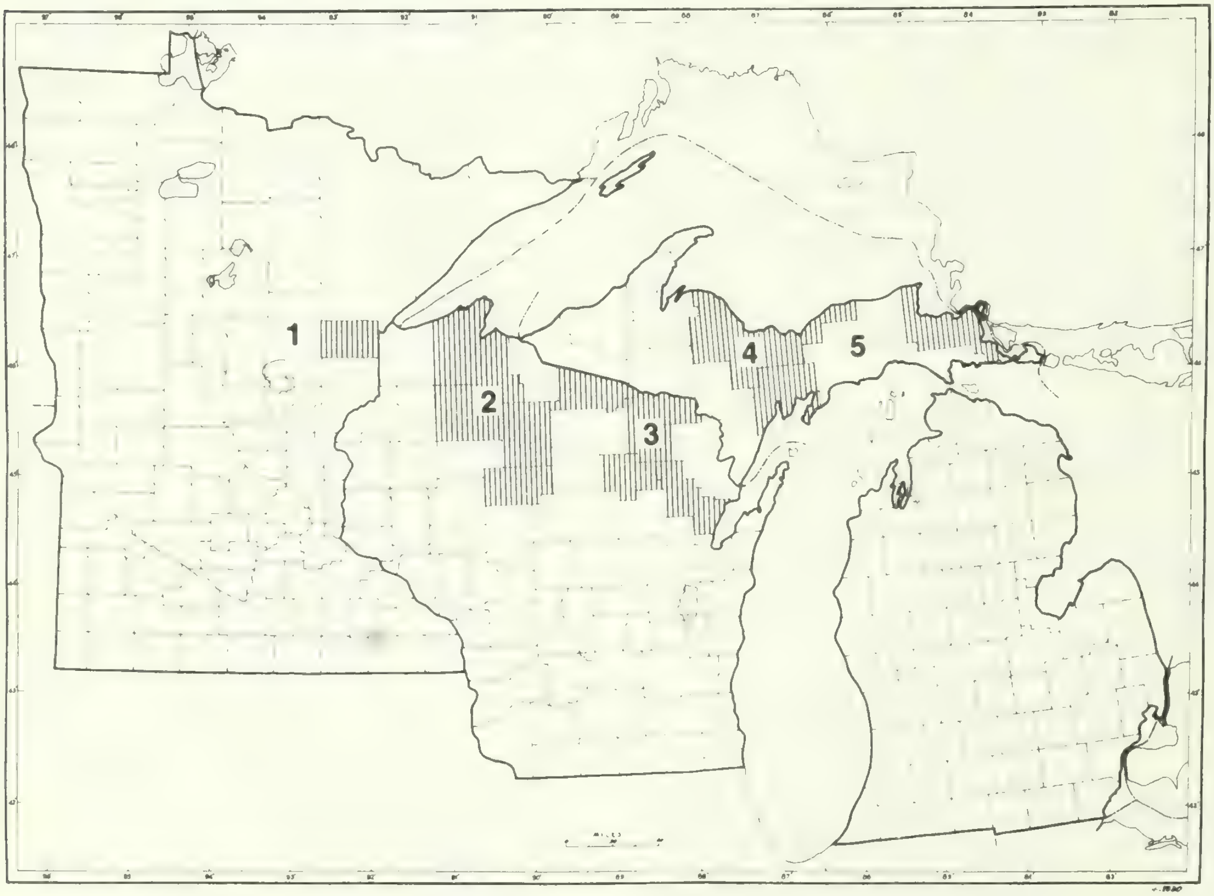

Figure 1.—*Geographical location of the five sources of permanent growth plot data used for independent tests of the projection system.*

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[1] *We thank Dietmar Rose and the staff of the Cloquet Forestry Center for making past measurement data available and for assistance in making a measurement in 1976.*

Table 1.—*Distribution of 785 permanent forest growth plots used for model validation by age and site within 12 forest types in the Lake States (site class 30 ranges from 25 to 34, 40 from 35 to 44, etc.)*

JACK PINE

Age :	Site index class						: Total
class:	30	40	50	60	70	80	
0-20		1		3			4
21-30		2			1		3
31-40			3	3	2		8
41-50		4	3	4	5		16
51-60	1	3	3	13	2		22
61-70			2	10	2		14
71-80			8	10			18
81-90			2	6			8
91-100			1				1
100+			1				1
Total							95
WHITE SPRUCE-BALSAM FIR							
0-20			2	2	2		6
21-30		1				1	2
31-40		2	2	1	1		6
41-50		2	4	7	2		15
51-60		3	5	2	2		12
61-70		1	6	6			13
71-80			5	5			10
81-90	1		3	2			6
91-100	1		1				2
100+	1	1					2
Total							74
TAMARACK							
0-20	1						1
41-50			1				1
51-60		2	2				4
61-70			1				1
71-80	1			1			2
81-90		1	2				3
91-100		4					4
100+		3					3
Total							19
OAK-HICKORY							
31-40					1		1
41-50			1	1	1		3
51-60			1	2			3
Total							7

RED PINE

Age :	Site index class						: Total
class:	30	40	50	60	70	80	
21-30			2		1		3
31-40			1	5	9	1	16
41-50			1	5	2	1	9
51-60			3	3	2		8
61-70	1		5	9	1		16
71-80		2	6	4			12
81-90		1	3	2			6
91-100		1		1	1		3
100+		1	4	6			11
Total							84
BLACK SPRUCE							
0-20		1					1
31-40		3					3
41-50	3						3
51-60	1	1	1				3
61-70	1	4	1				6
71-80	5		1				6
81-90	2	1					3
91-100	1	4	1				6
100+	7		1				8
Total							39
LOWLAND HARDWOOD							
31-40					1		1
61-70			1				1
91-100		1					1
100+	1						1
Total							4
QUAKING ASPEN							
0-20	1	1	3	12	9	2	28
21-30			2	1	2		5
31-40			2	4	5		11
41-50		1	7	12	16	4	40
51-60		2	9	5	7		23
61-70			1	3	2		6
71-80				2			2
81-90			1				1
91-100			1				1
100+	1						1
Total							118

WHITE PINE

Age :	Site index class							: Total
class:	30	40	50	60	70	80	90	
31-40		1		1	1			3
51-60			1	2	2			5
61-70			1	2				3
71-80		1	1					2
100+				1				1
Total								14
NORTHERN WHITE-CEDAR								
21-30			1					1
31-40	2	1		1				4
41-50	1		1					2
51-60	1	3	3					7
61-70	9	2	1					12
71-80	1	1						2
81-90	1							1
91-100	3							3
100+	10	3	1					14
Total								46
NORTHERN HARDWOOD								
0-20			1		2	1		4
21-30			1	1			1	3
31-40				1	7	2		10
41-50			3	11	22	1		37
51-60		1	9	25	11			46
61-70			4	13	105	1		123
71-80			1	3	1			5
91-100				1				1
100+	1		3	2	1			7
Total								236
PAPER BIRCH								
0-20			1	2				3
21-30	1				1			2
31-40			1		1	1		3
41-50		1	1	5	1			8
51-60	1	1	5	5	2			14
61-70			2	5	1			8
71-80			3	2	1			6
91-100			2					2
100+		1	1	1				3
Total								49

(2) use the first set of diameter measurements to start the projection,

(3) remove a tree from the projection tree list when it has been observed to have been cut,

(4) add a tree to the list of trees being projected when it is observed to be an ingrowth tree, and

(5) write an output file that contains observed and predicted diameter and status for each tree present on a plot at the first measurement. This is done for up to three points in time.

growth trees are not written on the output file (tep 5) for comparing observations and predic- tons. They are included in the projection process, wever, because in some cases ingrowth trees mprise a major part of the stand by the time of e final observation. Ignoring them could cause rious overestimation.

Analysis of the information produced at step 5 proceeds in two directions: (1) analysis for accuracy, and (2) analysis for precision.

The accuracy analysis is based on all the plots that occur in a forest type. We compare the predicted and observed mean stand diameter, trees per acre, and basal area per acre in a forest type by forming the ratio

$$\frac{\text{predicted mean stand attribute for the type}}{\text{observed mean stand attribute for the type}} .$$

Clearly, ratios consistently greater than one indicate overprediction (positive bias), and those consistently less than one indicate underprediction (negative bias). Caution is needed in interpreting ratios where the observed attribute (the denominator of the fraction) is very small and both observed and predicted are expressed as integers.

The precision analysis is needed to assess the repeatability of the estimated ratios for each type. Here we compute for each plot in a forest type the ratio of predicted to observed variable (mean stand diameter, trees per acre, basal area per acre), the mean ratio over all plots, and a standard deviation of the ratios.

Conceivably the projection system could, at 10 years, have a positive bias of exactly 6 percent for every plot in a forest type. This would not be an accurate predictor but would be precise. Lack of accuracy can, of course, be corrected. Lack of precision cannot be easily corrected. Rather, it indicates a general inability of the underlying model to capture the essence of the processes underlying stand dynamics.

To test the method of assembling the parts of the system (error type 2b) we used selected forest properties from the calibration data base, and did an accuracy analysis only. To test the applicability of the numerical constants to other forests in the Lake States region (error type 2c) we used the five properties in the validation data base (fig. 1), and did both an accuracy and precision analysis. In both cases, we based our analysis on all plots in a property regardless of their stocking level; plots having as few as three or four trees were used as well as fully stocked plots. Clearly, failure to satisfactorily pass the test on method of combining system parts makes the other test largely academic. Finally, it should be noted that the plots are typed by the projection program (Hahn and Brand 1979), and that trees of several species may be present on a plot, not just trees of the species the type name bears.

TEST RESULTS AND DISCUSSION

This section is broken into two parts; the first gives the results of testing the manner of combining system parts, and the second tests the applicability of the complete system, including values of numerical constants, to other forests of the Lake States.

Combining the System Parts

The results of tests are shown in figure 2. The model seems to predict mean stand diameter better than either number of trees or basal area. This is not surprising, since an error in predicting number of trees—even if diameter is predicted exactly—will usually cause an error in predicting total stand basal area.

Even so, the three ratios for most species are gratifyingly close to one at most points in time. Several points can be made based on the contents of figure 2:

(1) Predictions for Minnesota jack pine are decidedly better than those for Lower Michigan when the evaluation is based on mean stand diameter and total stand basal area. However, the model estimates number of trees better for Lower Michigan stands.

(2) Predictions for Minnesota and Wisconsin red pine plantations and natural stands are quite good, although nearly all show ratios somewhat greater than one.

(3) White pine mean stand diameter is predicted fairly well. The mean d.b.h. for the Minnesota source is underestimated, while that for the Wisconsin source is somewhat overestimated. Urenholdt trees per acre after 22 years is off some (23 percent), but trees per acre at the other locations are quite good.

(4) Only one small plantation was available to calibrate the system for white spruce. Even after 25 years the predictions are good.

(5) Predicted values for the balsam fir type are less than the observed values. The average stand diameter prediction gets progressively worse for the first 18 years, but then improves over the remaining 7 years of observations.

(6) Both average diameter and number of trees are underestimated for the black spruce and northern white-cedar types. Combined, these greatly underestimate basal area. Interestingly, most of the prediction error occurs in the first 10- to 13-year period. Thereafter the prediction essentially parallels the observation.

(7) Average diameter for test plots in the northern hardwood type is, for the most part within ± 4 percent of the observed. An exception is the Dundee timber harvest forest which overestimates average diameter by 12 percent after 27 years. Perhaps the severest test of the projection system occurred

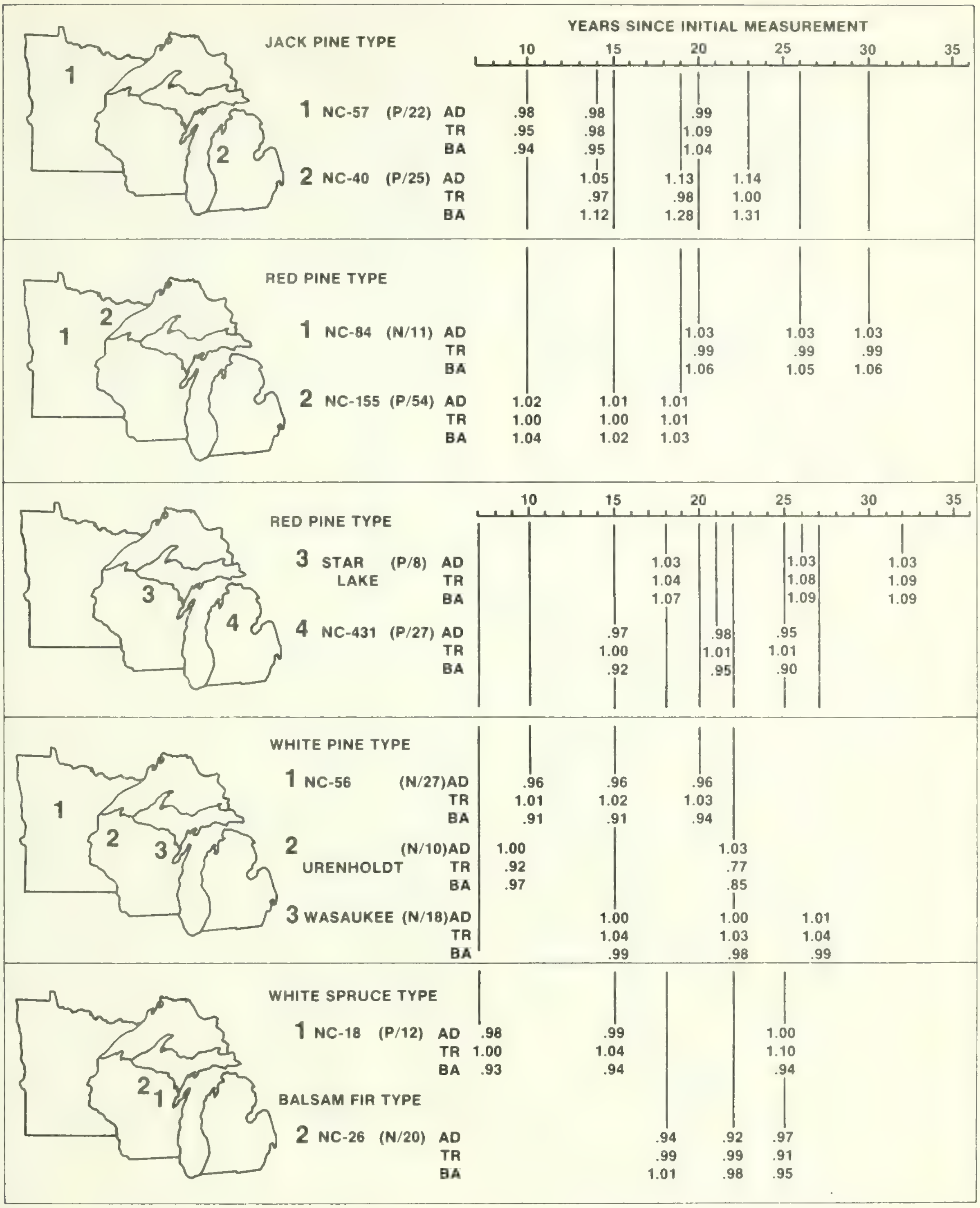
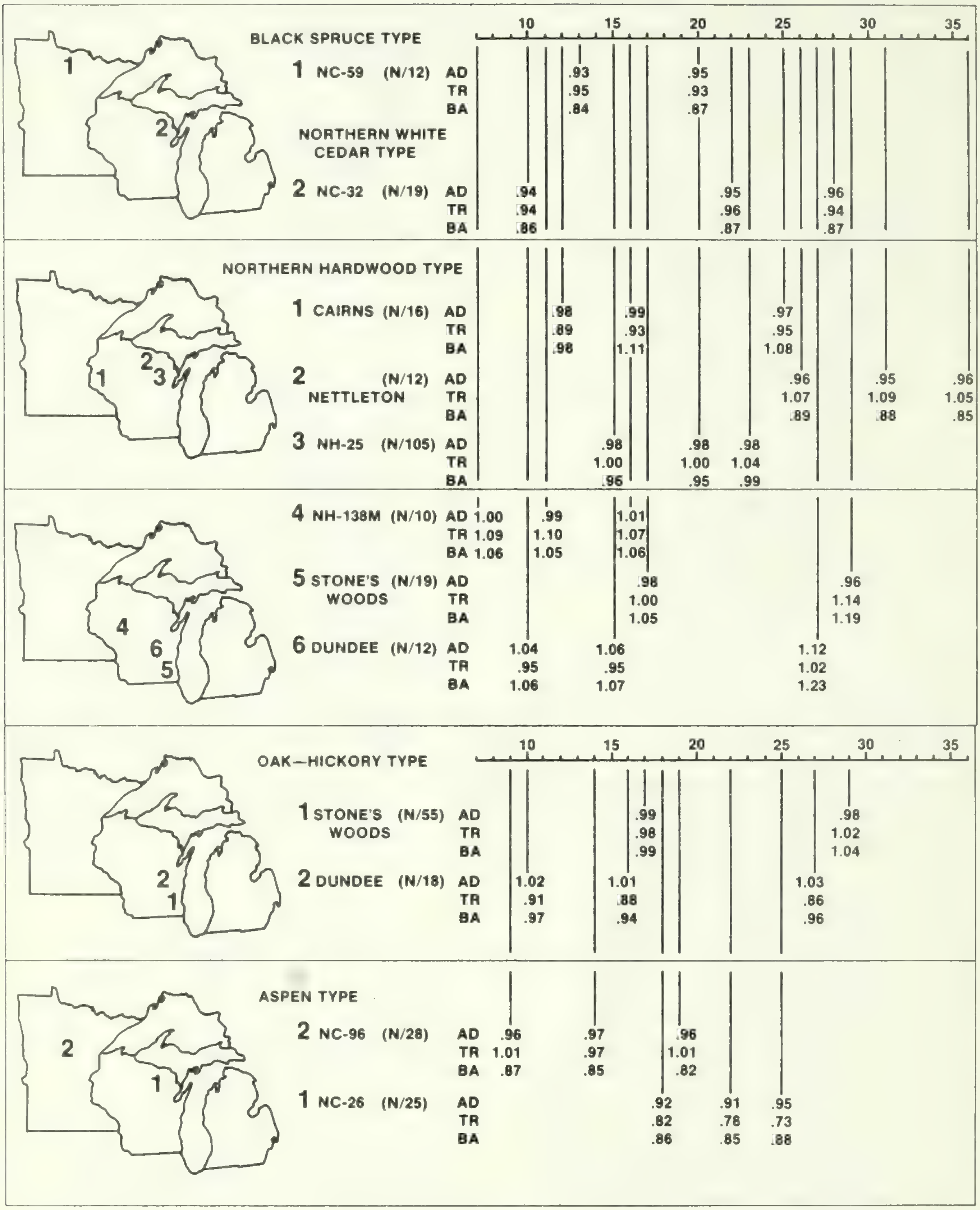


Figure 2.—*Test results of accuracy analysis of method of combining system parts. Each forest property is identified by name or number, plantation (P) or natural (N) stand and number of plots used in the comparison. Criteria for comparison are mean stand diameter for the type (AD), mean trees per acre for the type (TR), and mean stand basal area (BA) per acre for the type. Maps show approximate location of each property in Lake States. Ratios are computed as*

$$\frac{\textit{predicted mean stand attribute for a forest type}}{\textit{observed mean stand attribute for a forest type}}$$

Figure 2. — (continued)



with the Nettleton plots. The average stand diameter of the first measurement was between 1 and 2 inches. Even though projections were made for 36 years, the estimated mean stand diameter was within 4 percent of the observed.

(8) Predictions for the oak-hickory type, as found in southern Wisconsin, are reasonably good, although there is a tendency to overestimate mortality on the Dundee timber harvest forest.

(9) The Minnesota aspen type is reasonably well predicted for both average diameter and number of trees. The fact that basal area is underestimated so much is probably due to allocating too much of the diameter growth to small trees. The Wisconsin aspen comes from the same study as the balsam fir test. The 25 plots under test here probably had a large component of balsam fir. As with the 20 plots in the balsam fir type, mortality is overestimated and the average diameter is underestimated.

Tests on Independent Data Sets

Accuracy analysis

Five different data sets form the basis for these tests (fig. 1). The 266 Cloquet plots have been measured four times. The ratios of predicted to actual stand attributes is shown in table 2 for 5, 10, and 17 years after the initial measurement. Ratios

Table 2.—*Summary of Cloquet Experimental Forest test showing ratios of projected to actual mean plot diameter, trees per acre, and basal area per acre for the type totals converted to a per-acre basis (Cloquet plots are all 1/7 acre, fixed-radius)*

Forest type	No. of plots	Years after initial measurement								
		5	10	17	5	10	17	5	10	17
		(ratio of predicted to actual mean plot diameter)			(ratio of predicted to actual number of trees per acre)			(ratio of predicted to actual basal area per acre)		
Jack pine	43	1.02	1.03	1.04	1.02	1.03	1.06	1.05	1.09	1.13
Red pine	53	.99	.99	.98	1.00	.99	.99	.99	.97	.96
White pine	6	1.00	.99	.96	1.04	1.11	1.20	1.02	1.03	1.01
W.spruce-fir	37	1.02	1.03	1.04	1.08	1.12	1.26	1.12	1.19	1.37
Black spruce	29	1.01	1.03	1.05	1.05	1.09	1.18	1.07	1.14	1.32
N.w.-cedar	15	1.01	1.02	1.04	.99	1.01	1.03	1.01	1.06	1.12
Tamarack	15	1.02	1.03	1.06	.97	.97	.97	1.01	1.04	1.09
Lowland hdwd.	2	1.00	1.01	1.01	1.13	1.07	1.39	1.09	1.00	1.26
N. hardwood	2	1.01	1.05	.92	1.00	1.00	1.33	1.02	1.10	1.20
Aspen	32	1.02	1.05	1.07	.93	.93	1.00	.97	.99	1.11
Paper birch	26	1.02	1.03	1.04	1.03	1.03	1.01	1.06	1.09	1.10

Table 3.—*Summary of NH-2 test projection for the northern hardwood type (NH-2 plots are 1/10 acre, fixed-radius)*

Number of plots	Years after initial measurement								
	7	8	11	7	8	11	7	8	11
	(ratio of predicted to actual mean plot diameter)			(ratio of predicted to actual number of trees per acre)			(ratio of predicted to actual basal area per acre)		
37	1.00	—	.99	.99	—	.99	1.02	—	1.00
62	—	.99	—	—	.98	—	—	.97	—

Table 4.—*Summary of 10-year national forest test projections (all comparisons are based on repeated measurements of variable radius 10-point cluster plots)*

	Chequamegon				Nicolet				Hiawatha			
Forest type	No. of plots	D.b.h.	Trees	Basal area	No. of plots	D.b.h.	Trees	Basal area	No. of plots	D.b.h.	Trees	Basal area
Jack pine	7	1.04	1.02	1.09	5	1.06	1.18	1.23	20	1.09	1.03	1.16
Red pine	6	.99	1.11	1.00	6	1.02	.85	.96	12	.99	.94	.92
White pine	3	.96	1.09	.93	2	.93	.84	.87	3	.97	.99	1.00
W.spruce-fir	15	1.05	1.09	1.10	14	1.03	.91	1.05	8	1.02	1.53	1.16
Black spruce	2	1.13	.65	1.02	3	1.04	1.15	1.26	5	1.04	1.14	1.16
N.w.-cedar	6	1.00	1.00	1.02	12	1.02	.91	.96	14	1.04	.88	1.02
Tamarack	2	1.00	.75	.85	1	1.01	.95	1.01	—			
Oak-hickory	4	1.00	.70	.83	1	1.05	1.24	1.18	2	.95	.86	.87
Lowland hdwd.	2	1.00	.71	.99	—				—			
N. hardwood	45	1.01	.87	.95	54	1.00	.88	.94	36	1.01	.93	.96
Aspen	23	.98	.88	.98	44	1.02	.70	.97	17	1.04	.94	1.03
Paper birch	7	.96	1.18	1.09	6	.96	.72	.77	3	1.04	1.15	1.31
All types	122	1.01	.74	.95	148	1.01	.94	1.00	120	1.01	1.00	1.04

for the second growth northern hardwood study are shown in table 3. Thirty-seven plots had three measurements and 62 had only two measurements. The three national forests had two measurements only, so only one ratio is presented for them in table 4.

The Cloquet test shows 8 of 11 types have overestimates of mean d.b.h., 9 of 11 have overestimates of trees per acre and 10 of 11 have overestimates of basal area. Although the mean diameter overestimates are not serious, they are notable for their consistency and regular progression; for example, 1 or 2 percent after 5 years, 2 or 3 percent after 10 years, and 4, 5, or 6 percent after 17 years for white spruce-fir, black spruce, northern white-cedar, tamarack, and paper birch types. In fact, all types except red pine, white pine, and northern hardwoods have nearly the same progression of accuracy decay in predicting mean diameter. There is close agreement in both the type of error (over- or underestimate) and progression of accuracy decay when evaluating the system on number of trees. Exceptions appear to be the white pine, tamarack forest types and northern hardwoods. The ratios for predicted and observed basal area follow closely the estimates of mean diameter and number of trees.

The Cloquet results confirm earlier forecasts that the projection system would overestimate observed variables. This forecast was based on personal observations of the field remeasurement crew on the quantity of large shrubs and small trees present on Cloquet plots. Any competing vegetation that has affected growth of the trees on the plot but is not a part of the recorded observations will result in overestimates.

The major independent test for northern hardwoods was based on the repeated measurements of a study (NH-2) in Michigan's Upper Peninsula (table 3). The ratios are close to one in almost every case, and hence warrant little discussion.

The Chequamegon, Nicolet, and Hiawatha National Forest plot data cover a period of 10 years (table 4). These plots differ from the Cloquet and NH-2 plots in three ways: the plots are 10-point clusters of variable radius plots, the trees are measured down to 1.0 inch diameter, and the remeasurement occurred 10 years after the initial measurement. Most notable of the Chequamegon results are the relatively large overestimates of mortality in the black spruce, tamarack, oak-hickory, lowland hardwood, northern hardwood, and aspen types. One might discount overestimates in the first four types as chance occurrences because of the low plot numbers. We feel it is more likely because the mean plot diameters tend to be small, especially on the black spruce type, and because the number of trees represented by a small tree is larger than the number represented by a large tree (recall these are variable-radius plots). Thus, if the projection should assign a mortality status to a very small tree, it may mean that 100 trees per acre (its tree factor) are considered to have died. This points up one of the major differences in the way fixed- and variable-radius plots are projected.

The Nicolet also shows low estimates of numbers of trees for the aspen and paper birch forest types. The Hiawatha shows a 53-percent overestimate of trees per acre for the white spruce-fir type. Most of this difference is attributable to three of the eight plots. Because we are underestimating mortality on some plots by as much as 242 trees per acre in only 10 years, it is apparent that some variable other than competition is dominating the mortality process.

Precision analysis

The precision analysis, based on the Cloquet and NH-2 data sources, differs from the accuracy analysis in two respects:

(1) we consider only the ratio of predicted to actual mean stand diameter (ratios for number of trees and basal area have been computed but are not included here), and
(2) we consider the ratio for each individual plot in computing the mean and standard deviation of the ratios over time for for each measurement following the first.

Again, the analysis is organized by forest type. Figure 3 contains graphs for nine of the Cloquet types (lowland hardwood has been omitted), and figure 4 shows the mean and standard deviation at the two points in time for the northern hardwood type from NH-2.

Our concern with this analysis is with the pat-

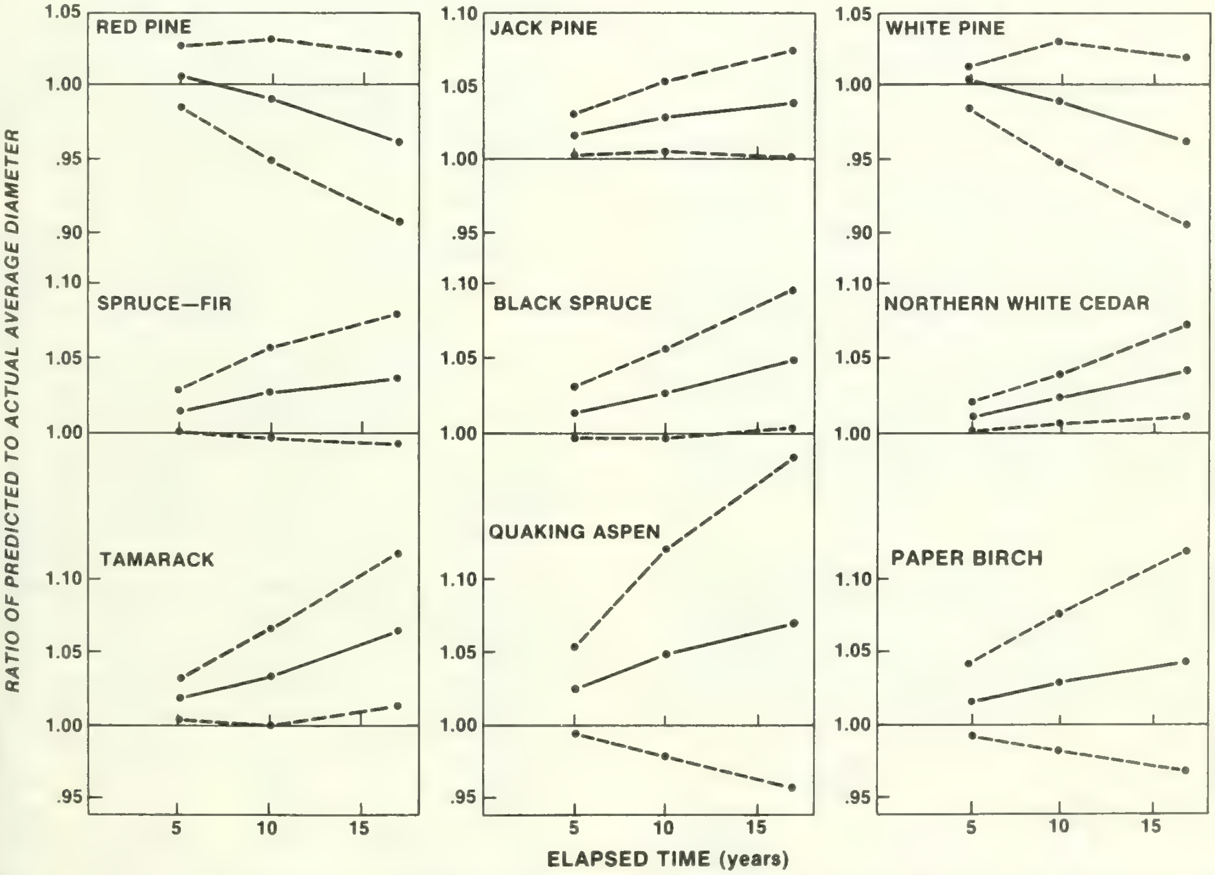
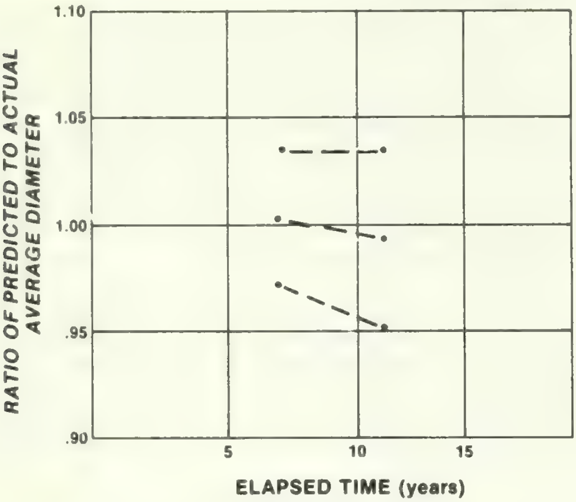


Figure 3.—*Pattern of ratios and standard deviation of ratios of predicted to actual mean plot diameter for nine forest types on the Cloquet Experimental Forest, Minnesota. Standard deviations are shown in dashed lines, means in solid lines.*

Figure 4.—*Pattern of mean ratios and standard deviation of ratios of projected to actual mean plot diameter for the northern hardwood type.*



tern created by plotting the mean ±1 standard deviation over time. Specifically, we look at (1) the closeness of the mean ratio to 1.00 at each time, and (2) the magnitude of the standard deviation and its relation to time since the initial measurement. Concern number 2 is particularly important.

Figures 3 and 4 show that all mean ratios are within ±7 percent of 1 after 17 and 11 years, respectively. For most types the ratios begin near 1 at 5 years and increase linearly to the value at 17 years. Jack pine, white spruce-fir, quaking aspen, and paper birch have noticeable concave patterns to the mean ratio. Tamarack and northern white-cedar show signs of a convex pattern. In all cases except the red and white pine types, extrapolation backward to the initial measurement would yield a ratio near 1.0.

Comparing the standard deviation magnitude shows that northern white-cedar is smallest, with black spruce, white spruce-fir, and jack pine also low. Quaking aspen has the largest standard deviation, followed by paper birch, red pine, and white pine.

The trend in standard deviation magnitude over time shows three patterns: (1) linear, (2) concave, and (3) convex. We consider jack pine, paper birch, and black spruce to be linear. Red pine, white pine, aspen, and white spruce-fir are judged concave. Tamarack and northern white-cedar appear to exhibit more of a convex pattern. With only two points, a trend cannot be assigned to the northern hardwood type (fig. 4).

The least desirable standard deviation trend type would be convex; linear would be better, and the most desirable would be concave. Trend type alone, however, is not sufficient to rate the goodness of projections by forest type, because it is confounded with standard deviation magnitude and the ratio trend itself. For example, we rate white pine, red pine, aspen, and white spruce-fir as having the best standard deviation trend type (concave), but none of these rates low on standard deviation magnitude. The northern white-cedar type shows a linear trend type and it has the lowest standard deviation. Because of these conflicting relations (fig. 3) it is not possible to say which type is projected the best (as measured by predicted vs. actual mean diameter). It is, however, possible to identify three candidates for "poorest" rating: quaking aspen, paper birch, and tamarack. A more definitive analysis could probably be made if numbers of trees were also included.

Table 5 summarizes the results of the precision analysis based on individual plot ratios of predicted to actual mean diameter for each forest type.

Table 5.—*Summary of precision analysis findings for projections of mean stand diameter (all results are based on Cloquet Forest plot data except the northern hardwood type, which is based on NH-2 from Upper Michigan)*

Forest type	Trend in ratio of projected to actual mean plot diameter	Comparative overall magnitude of standard deviation	Time trend in magnitude of standard deviation
Jack pine	linear	small	linear
Red pine	concave	medium	concave
White pine	concave	medium	concave
White spruce-fir	concave	medium	concave
Black spruce	linear	small	linear
N. white-cedar	convex	small	convex
Tamarack	convex	medium	convex
Northern hardwood	NA[1]	medium	NA[1]
Quaking aspen	concave	large	concave
Paper birch	linear	large	linear

[1] Not applicable because only two points in time are availabl

SUMMARY

Tests of the projection system were based on omparisons of predicted and actual mean diame- ers, number of trees per acre, and basal area per cre for two data sets: (1) selected properties from he calibration data base, and (2) an independent lata base. A summary of the important findings, rganized around two central questions, is given elow.

I. Is the method of combining system parts sat- sfactory?

1. The method of combining system parts (potential, modifier, allocation rule, mortality, etc.) is satisfactory.
2. Many of the calibration data base properties are projected very well for up to 30 years (fig. 2).
3. Properties with small trees are generally less well projected (e.g., NC-26, NC-32, NC-18, Nettleton, NC-59, fig. 2) than those with large trees.
4. Sizable growth rate differences for jack and red pine appear between Lower Michigan and Wisconsin-Minnesota. If validated by further checks, this indicates the need for separate coefficients for at least Lower Michigan.
5. Projections of average diameter are better than numbers of trees, which are better than basal areas.

II. Is the projection system applicable to other areas in the Lake States?

1. The projection system did a reasonably good job of projecting plots from Minnesota, Wisconsin, and Upper Michigan. These plots had not been used to calibrate the system.
2. Consistent positive bias (as much as 6 percent in 17 years) was found in predictions of mean d.b.h. for several cover types on the Cloquet Forest in Minnesota.
3. Variable-radius plots (10-point cluster design of Forest Survey) can be satisfactorily projected for 10 years, although mortality is sometimes overestimated for plots with many small trees.
4. No discernible deficiencies were found in projection capabilities for any species in the independent data sets as geographical location changed. It should be noted that we had no independent data set from Lower Michigan.
5. The standard deviation of the ratio of projected to actual mean plot diameter showed three types of trends when plotted over years since the original measurement: concave, linear, and convex. Northern white-cedar and tamarack forest types showed the least desired (convex) trend. Red pine, white pine, white spruce-fir, and quaking aspen showed the most desired (concave) trend.

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PRECIPITATION AND TEMPERATURE TRENDS IN THE LAKE STATES FOR SELECTED WEATHER STATIONS

Jerrilyn LaVarre Thompson, *Forestry Technician*

The purpose of this report is to summarize trends of precipitation and temperature at selected locations in the Lake States and discuss these trends and their possible impact on the calibration of a forest growth projection study. Substantial differences in the rainfall or temperature between the period used for calibration and future periods could have an effect on the accuracy of the projections.

Previous work on the impact of climate on tree growth has indicated a close correlation between precipitation and radial stem growth (Dils and Day 1952). The transition from wet years to dry years induces a gradual, rather than sharp, decrease in tree growth, reflecting a lag in soil moisture response to decreased rainfall. The reverse transition from dry to wet periods produces immediate growth response because soil moisture is replenished more rapidly than it is lost by evapotranspiration. Temperature also affects tree growth, primarily because it regulates growth initiation in the spring (Dils and Day 1952). However, we have made no attempt to correlate climate data and tree growth in this report.

DATA SOURCES

Most of the data in this report were obtained from records provided by the Minnesota State Climatology Office, 1903 Hendon Avenue, St. Paul, Minnesota 55108. Additional data were obtained through correspondence with Forest Service personnel in Michigan.

Precipitation and temperature data for the 6-month period, April through September, were compiled by month for 11 weather stations throughout Minnesota, Michigan, and Wisconsin from the year of each station's establishment through 1976 (fig. 1). The criterion for weather station selection was the station's proximity t permanent studies of forest growth.

In all but two cases, both precipitation an temperature were recorded at each station. At th Cass Lake, Minnesota station, only precipitatio was recorded; at the Virginia, Minnesota station temperature was the only variable recorded.

Precipitation was recorded by month at eac station from April through September from th year of station establishment through 1976. Temperature was not recorded in the annals monthl until 1931; consequently, the values prior to 193 are the April through September averages fro the date of station establishment through 1930.

Minnesota and Wisconsin temperature value were recorded by month from 1931 through 197 Michigan monthly temperature values were no recorded until 1941 at Cadillac, and 1951 at Allegan, Grayling, and East Tawas. No temperatur information was available for Grayling or Eas Tawas until 1931; from 1931-1951, only the April through-September average was available. April through-September temperature averages wer recorded for Cadillac and Allegan from statio establishment to 1941 and 1951, respectively.

GROWING SEASON

Prior to discussing the data analysis, the ter "growing season" as used in this text should b defined. Usually the growing season is describe as the period between the last killing frost in th spring and the first killing frost in the fall. Som factors that determine whether a plant will b killed by frost are species, age, time of year, an duration and rate of freezing (Moran and Morga

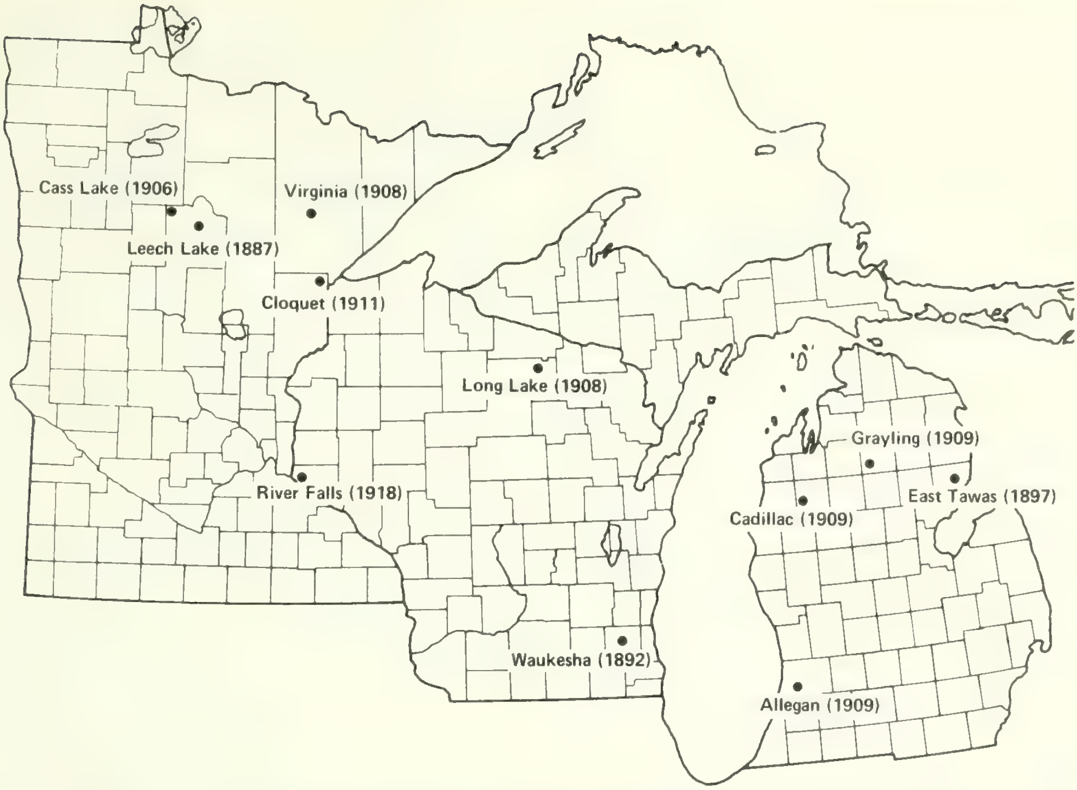

Figure 1.—*Location and date of establishment of meteorological stations. Monthly (April to September) precipitation and temperature information was recorded from each station, except Cass Lake, where only precipitation was recorded, and Virginia, where only temperature was recorded.*

976). The Weather Bureau commonly designates he growing season as the "freeze-free" period, hen minimum temperatures are greater than 2°F. (0°C.). Another measure employs a 28°F. 2°C.) free period, which accommodates for local emperature variations.

In the Lake States the frost-free period gener- lly extends from April through September. oran and Morgan (1976) cite the three Wisconsin tations used in this study as having 28°F. free eriods that range from 110 to 195 days. The Min- esota stations, Virginia, Cloquet, and Leech ake, have 28°F. free seasons that extend from 104 159 days (Baker and Strub 1963). While most ee growth occurs in June and July, it does begin s early as April and can continue until Septem- r. Therefore, in this study we have defined the rowing season as the 180-day period from April rough September, to include all tree growth oc- rring in any year.

DATA ANALYSIS METHODS AND RESULTS

To prepare the information for analysis, several steps were taken. The monthly precipitation data were added to obtain growing season rainfall totals. Average temperatures for each growing season were also calculated.

Five-year averages for both precipitation and temperature were calculated for each station from its date of establishment through 1976 (figs. 2 and 3). "Even" 5-year intervals were used for ease of manipulation (i.e., 1901-1905, 1906-1910, etc.). The first average for a station may include more than five yearly measurements to accommodate this scheme. For example, Allegan, Michigan precipitation data began in 1909, but the first "even" interval is 1911-1915; consequently, the first interval is 7 years, from 1909-1915. All subsequent averages are 5 years, except for the last interval,

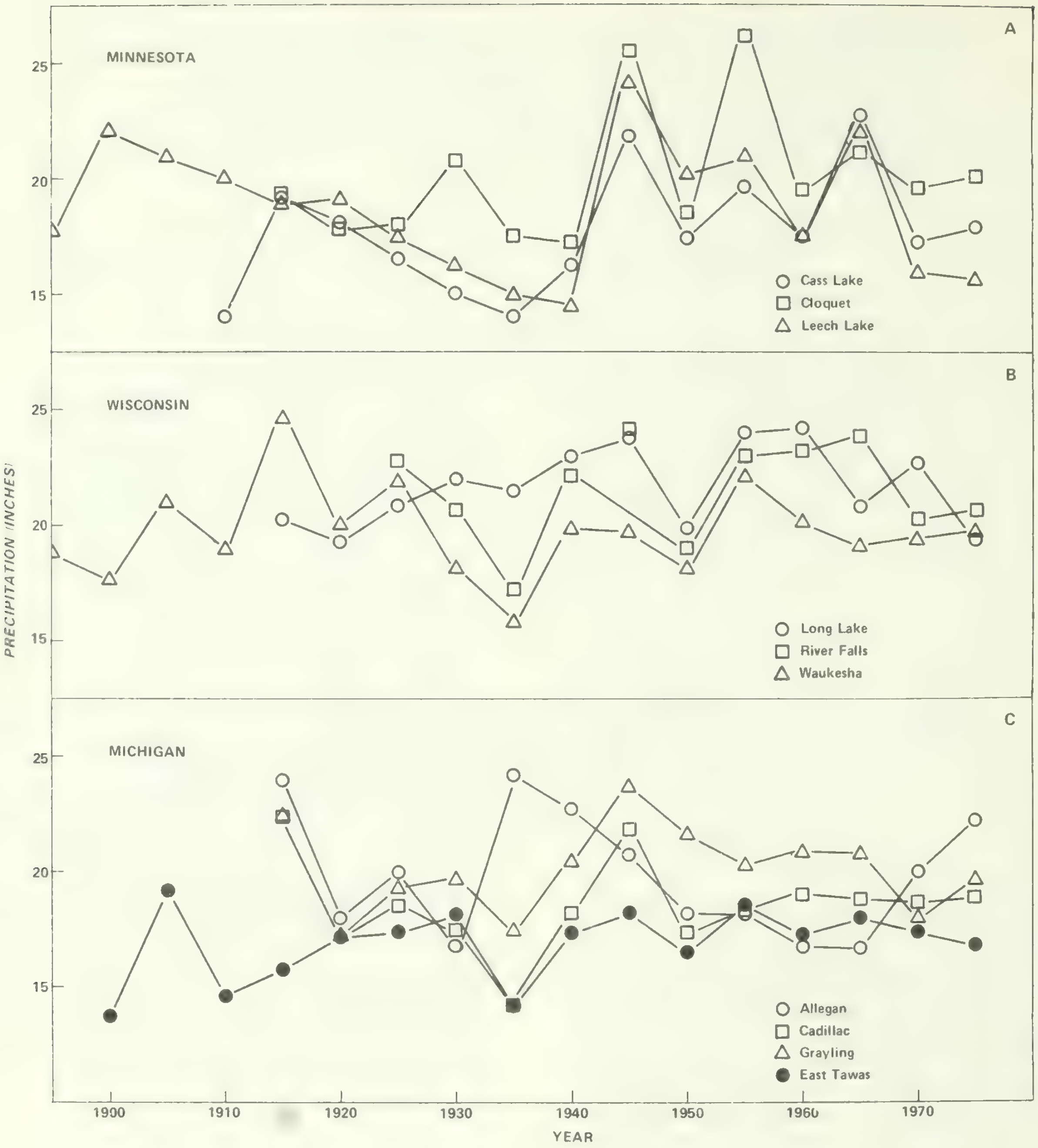

Figure 2.—*April-to-September precipitation trends in the Lake States. Five year averages from selected weather stations were plotted at the endpoint of each interval.*

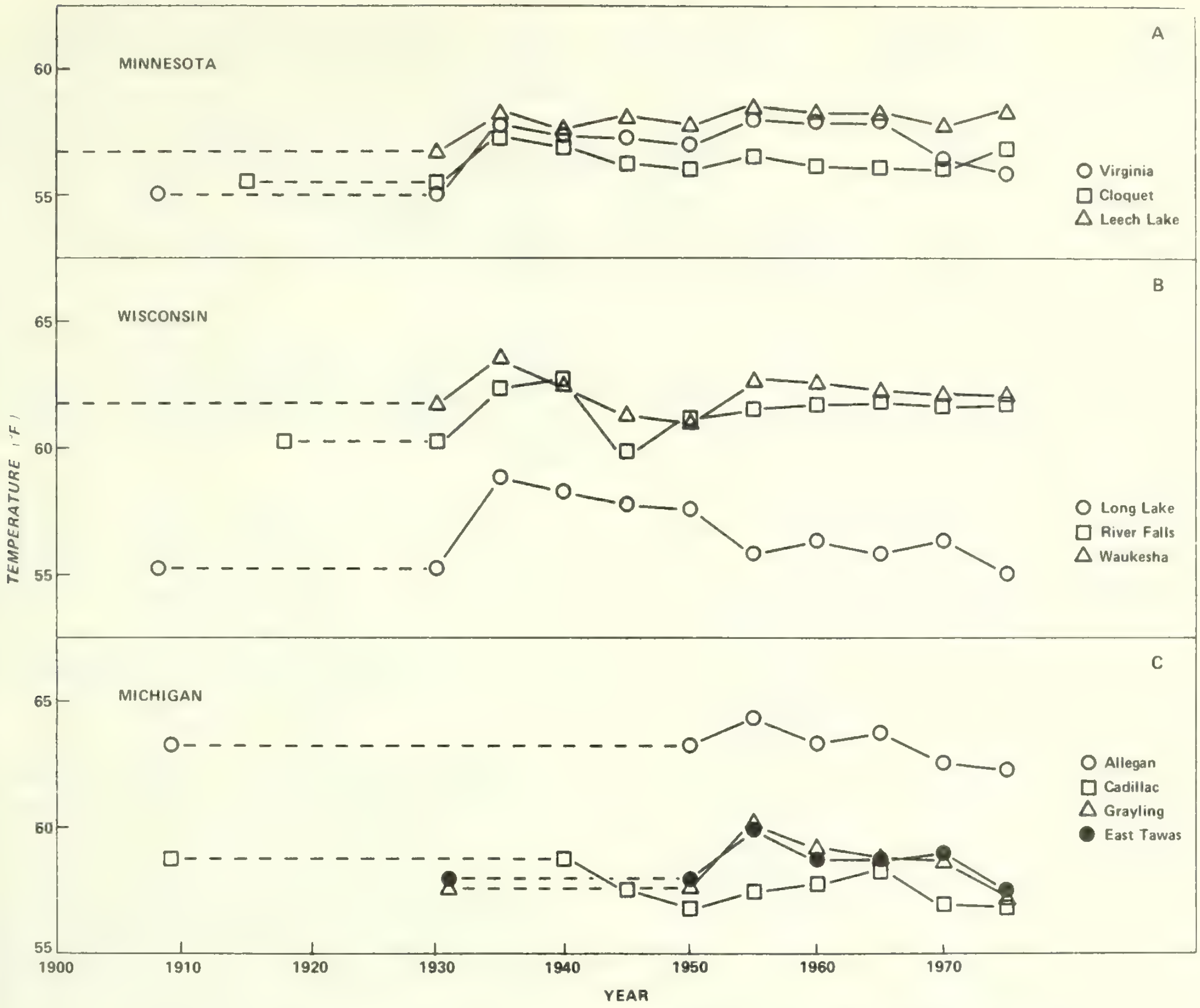

Figure 3.—*April-to-September temperature trends in the Lake States. Five year averages from selected weather stations were plotted at the endpoint of each interval. Dashed lines indicate the average for periods when monthly or yearly averages were missing.*

1971-1976. The average for an interval is plotted at the endpoint of that interval.

Trends in precipitation and temperature were analyzed for three periods: (1) station establishment through 1976; (2) station establishment through 1935; and (3) 1936-1976. The period 1936-1976 encompasses the interval when field measurements for the forest growth projection study were taken, and is referred to as the calibration period (Christensen *et al.* 1979). In addition, the months of June and July were analyzed separately for the calibration period. Soil moisture is critical during these months, because it is then that soil moisture deficits are first apparent, and it is also the time when most growth occurs (Fraser 1962).

Yearly fluctuations in precipitation for the various weather stations are large, yet there are some notable trends. For example, in Minnesota from 1911 through 1976, growing season precipitation at the Leech Lake, Cass Lake, and Cloquet stations increased slightly overall, as shown by linear regression analysis. Until 1940 a decrease in rainfall was recorded for all three stations. Cass Lake showed a marked increase in precipitation from 1941 to 1976 (fig. 2a). Leech Lake showed an increase in rainfall from 1940 to 1945, but a gradual decline from 1946 to 1976.

Cloquet showed a decrease in precipitation from 1940 to 1976. From 1936 to 1976 for June-July rainfall gradually increased at all three Minnesota stations.

In Wisconsin, precipitation increased from 1918 to 1976. From station establishment to 1976, the Long Lake and River Falls stations showed increasing rainfall amounts, but the Waukesha station recorded a decrease (fig. 2b). The period from station establishment to 1935 was generally drier than the period from 1936-1976. The 1936-40 interval marked an increase in rainfall for a decade. Since 1940, all Wisconsin weather stations have recorded an overall decrease in precipitation. For the June-July analysis, Long Lake and River Falls showed a decrease in the amount of rainfall, while Waukesha showed an increase.

In Michigan the overall trend from 1909 to 1976 was one of decreasing rainfall (fig. 2c). From station establishment through 1976, Allegan and Cadillac exhibited this downward trend; however, Grayling and East Tawas showed an increase in rainfall for the same period. From station establishment to 1935, East Tawas experienced progressively more rainfall, while the other Michigan stations experienced a drying trend. During the calibration period these trends continued. However, the June-July analysis showed decreasing precipitation at Grayling and increased precipitation at the other stations.

In the Lake States overall, the period from the various stations' establishment to 1935 was generally drier than the calibration period (1936-1976). Following 1935, which marked the end of the "Dust Bowl" era, precipitation increased for a decade throughout the Lake States. This was followed by a general drying trend through the 1976 growing season at all stations in the study, except at East Tawas and Cass Lake.

The average precipitation for the Lake States from station establishment through 1976 was 19.5 inches. From station establishment through 1935 the average was 18.7, and for the calibration period, 1936-1976, the average was 20.0 inches. Wisconsin had the highest averages: 21.0, 20.0, and 21.4 inches for the periods from station establishment-1976, station establishment-1935, and 1936-1976, respectively. Minnesota had an overall average of 18.7 inches, a station establishment-1935 average of 17.4, and a calibration period average of 19.5 inches. Michigan averaged 18.9 inches overall, 18.6 inches from station establishment-1935, and 19.1 inches during the calibration period.

Temperature trends for the study period did not fluctuate as much as precipitation patterns. Station temperature values were fairly constant through time, but varied by location. Allegan had the highest calibration period average, 63.2°F. (17.3°C.), followed by Waukesha and River Falls with 62.0°F. (16.6°C.) and 61.5°F., (16.4°C.), respectively. Cloquet had the lowest average, 56.3°F. (13.4°C.).

Because 5-year averages in Minnesota and Wisconsin were not available prior to 1931, and between 1941 and 1951 in Michigan, the information on temperature trends is limited to the calibration period.

Each State showed a slight cooling trend for the calibration period when linear regression analysis techniques were applied. On a station-by-station basis, however, only six stations exhibited a cooling trend. The other four stations— Leech Lake, River Falls, Waukesha, and Cadillac— indicated slight warming trends (fig. 3).

When June-July temperatures were examined, they were similar to the growing season trends at all stations except Cloquet, which showed gradually increasing June-July temperatures.

The average Lake States growing-season temperature for the period from station establishment to 1976 and for the calibration period was 58.9°F. (14.9°C.). The corresponding averages for these two time periods by State are as follows: Wisconsin— 60.1°F. (15.6°C.), and 60.0°F. (15.5°C.); Michigan—59.5°F. (15.3°C.) for both periods; and Minnesota—57.0°F. (13.9°C.) and 57.1°F. (13.9°C.).

Although the data indicate downward trends for both precipitation and temperature during the growing season and an increase in precipitation for the months of June and July (table 1), these trends may not continue into the future.

IMPLICATIONS OF FINDINGS

Precipitation and temperature are external factors affecting tree growth. They fluctuate both yearly and over longer time periods.

It is logical to assume that short-term fluctuations of both precipitation and temperature are normal and that their overall effect on forest able 1.—*Comparative growing season precipitation and temperature trends from Station establishment to 1976 and 1936-1976 (for the period 1936-1976, both the April to September and June and July trends are summarized)*

PRECIPITATION TRENDS

	Minnesota			Wisconsin			Michigan			
	Cass Lake	Cloquet	Leech Lake	Long Lake	River Falls	Waukesha	Allegan	Cadillac	Grayling	East Tawas
ation establ.- 1976 April-Sept.	increase	increase	decrease	increase	increase	decrease	decrease	decrease	increase	increase
936-1976 April-Sept.	increase	decrease	decrease	decrease	decrease	decrease	decrease	decrease	decrease	increase
June-July	increase	increase	increase	decrease	decrease	increase	increase	increase	decrease	increase

TEMPERATURE TRENDS[1]

	Cass Lake	Cloquet	Leech Lake	Long Lake	River Falls	Waukesha	Allegan	Cadillac	Grayling	East Tawas
ation establ.- 1976 April-Sept.	increase[2]	increase	increase	decrease	increase	increase	decrease	decrease	increase	increase
936-1976 April-Sept.	decrease[2]	decrease	increase	decrease	increase	increase	decrease	increase	decrease	decrease
June-July	decrease[2]	increase	increase	decrease	increase	increase	decrease	increase	decrease	decrease

Michigan temperature trends from 1941-1976 at Cadillac, and from 1951-1976 at other stations.

Virginia recording station.

rowth is minimal. These fluctuations are re- lected in seasonal growth variation. During years f abundant rainfall and warm temperatures, in- ividual trees or stands of trees put on more rowth. Conversely, sparse rainfall and cold or xtremely hot temperatures inhibit growth (Diller 935). If these periods of highs or lows are pro- nged, a marked difference in growth rates would e expected to follow.

Since the projection system is calibrated on measurements taken between 1938 and 1976, a very favorable period for tree growth in the Lake States, its use for projections into periods of unknown precipitation and temperature must be made with caution. If rainfall and temperature are higher in the future than during the calibration period, the probable result would be underestimation of tree growth by the models. If, on the other hand, the period following calibration is dry and cool or dry and exceptionally warm for an extended period of time, the models would probably overestimate actual growth.

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A collection of 12 papers describing the need, design, calibration data base, potential diameter growth function, crown ratio, modifier, and mortality functions, as well as a diameter growth allocation rule, management algorithms, computer program, tests, and Lake State climate during calibration.

OXFORD: 612:564(77). KEY WORDS: forest growth, simultaneous equations, Lake States, mathematical model, mortality, competition.

U. S. Department of Agriculture, Forest Service.

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Thirteenth Lake States Forest Tree Improvement Conference

The Thirteenth Lake States Tree Improvement Conference was held at the University of Minnesota, St. Paul/Minneapolis, August 21-23, 1977. The Lake States Forest Tree Improvement Committee want to express its gratitude to the University staff for an excellent meeting.

ANNOUNCEMENT

LAKE STATES and CENTRAL STATES FOREST TREE IMPROVEMENT COMMITTEES TO MERGE

To reduce the number of meetings, to provide larger, better attended meetings and in order to facilitate the publication of proceedings the Executive Committees of the Lake States and Central State Organizations have decided to merge. The new organization will be known as

NORTH CENTRAL TREE IMPROVEMENT ASSOCIATION

The merger will be finalized at the FIRST NCTIA MEETING to be held at the University of Wisconsin, August 21-23, 1979.

The LAKE STATES FOREST TREE IMPROVEMENT COMMITTEE was organized at Eagle River, Wisconsin in March 1953. Through 1977 the Committee conducted the following 13 Tree Improvement Conferences:

Lake States Forest Genetics Conference, Eagle River, Wis., March 31-April 1, 1953.

Proceedings, Lake States Forest Genetics Conference, March 31-April 1, 1953. Lake States Forest Expt. Stn, Misc. Rpt. 22, 83 pp. (Processed) 1953.

Second Lake States Forest Tree Improvement Conference, Wisconsin Rapids, Wis., August 30-31, 1955.

Proceedings, Lake States Forest Tree Improvement Conference, August 30-31, 1955. Lake States Forest Expt. Stn., Misc. Rpt. 40, 108 pp., illus. (Processed) 1955.

Third Lake States Forest Tree Improvement Conference, Grand Rapids, Minnesota, September 17-18, 1957.

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Fourth Lake States Forest Tree Improvement Conference, Ann Arbor, Michigan, October 6-7, 1959.

Proceedings, 4th Lake States Forest Tree Improvement Conference, Lake States Forest Expt. Stn., USDA, Forest Service Station Rpt. 81. 60 p. 1960.

Fifth Lake States Forest Tree Improvement Conference, Rhinelander, Wisconsin, September 19-20, 1961.

Proceedings of the 5th Lake States Forest Tree Improvement Conference, Lake States Forest Expt. Stn., USDA, Forest Service Station Pap. 48, 42 p. April 1962.

Sixth Lake States Forest Tree Imprvoement Conference, Grand Rapids, Minnesota, September 8-9, 1963.

Proceedings of the 6th Lake States Forest Tree Improvement Conference, Lake States Forest Expt. Stn., USDA, Forest Service. 90 p. August 1964.

Seventh Lake States Forest Tree Improvement Conference held jointly with Second Genetics Workshop of the Society of American Foresters, Hickory Corners, Michigan, October 21-23, 1965.

Joint Proceedings 2nd Genetics Workshop of the Soc. of American Foresters and the 7th Lake States Forest Tree Improvement Conference, USDA Forest Service Research Paper NC-6. 110 p. 1966.

Eighth Lake States Forest Tree Improvement Conference, Madison, Wisconsin, September 12-13, 1967.

Proceedings of the 8th Lake States Forest Tree Improvement Conference. USDA, Forest Service Research Paper NC-23, 60 p. 1968.

Ninth Lake States Forest Tree Improvement Conference, Grand Rapids, Minnesota, August 22-23, 1969.

Proceedings of the 9th Lake States Forest Tree Improvement Conference. USDA, Forest Service Research Paper NC-47. 34 p. 1970.

Tenth Lake States Forest Tree Improvement Conference held jointly with Seventh Central States forest Tree Improvement Conference, Madison, Wisconsin, September 22-24, 1971.

Joint Proceedings of the 10th Lake States Forest Tree Improvement Conference and the 7th Central States Forest Tree Improvement Conference. USDA, Forest Service General Technical Report NC-3, 61 p. 1973.

Eleventh Lake States Forest Tree Improvement Conference, Hickory Corners, Michigan, October 10-12, 1973.

This meeting was entirely devoted to field trips. No Proceedings were published.

Twelfth Lake States Forest Tree Improvement Conference held jointly with the Canadian Tree Improvement Association, Petawawa Forest Experiment Station, Chalk River, Ontario, August 18-22, 1975.

Proceedings of the 12th Lake States Forest Tree Improvement Conference. USDA, Forest Service General Technical Report NC-26. 206 p. 1976.

Thirteenth Lake States Forest Tree Improvement Conference, St. Paul/ Minneapolis, Minnesota, August 17-18, 1977.

The 12 Proceedings were all published by the North Central Forest Experiment Station, USDA, Forest Service (formerly Lake States Forest Experiment Station). The Experiment Station provided technical review and editorial services and covered all expenses connected with publications.

The Lake States Forest Tree Improvement Committee wishes to thank the North Central Forest Experiment Station for this great contribution to the Committees work and to Tree Improvement and Genetics Research in the Lake States.

Hans Nienstaedt
Executive Secretary
Lake States Forest Tree Improvement Committee

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PROMOTION OF FLOWERING IN THE PINACEAE [1] BY HORMONES -- A REALITY

Richard P. Pharis [2]

ABSTRACT.--The effectiveness of gibberellins as promotors of flowering in Cupressaceae and Taxodiaceae is historically reviewed, emphasizing that these groups of plants respond to polar gibberellins and produce sexual structures after exogenous application of GA_3. Species in Pinaceae, on the other hand, can be brought into flowering with non-polar gibberellin treatments. Admixtures of gibberellins applied with auxin and stimulatory cultural treatments such as strangulation, nitrate fertilization, root pruning, or drought stress are particularly successful. Each species, age, even each clone and each site may require highly "specific" treatments in forms of dosage level, frequency of application, hormone mixture, and adjunct cultural treatment.

In this paper I will discuss the effects of certain of the gibberellins on flowering of young seedlings, grafted ramets, and older trees in the Pinaceae. I will also give you some history of the work that went into obtaining the results. I do this for two reasons: One is to show you that the induction, or promotion of flowering in Pinaceae is not a simple procedure; gibberellins are not a patent medicine. You can't just walk through a seed orchard and spray the hormones on the trees and stand back and wait for the flowering. It takes a knowledge of the period of "sexual" differentiation, and may require other cultural treatments in addition to the hormones. Results from a given dosage rate, or application

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[1] This paper draws heavily on individual and collaborative work by the following: A. Dunberg, J. Glenn, G. Kiss, C. G. Kuo, W. Morf, J. Owens, R. M. Rauter, G. Sweet, R. Wample, and N. Wheeler.

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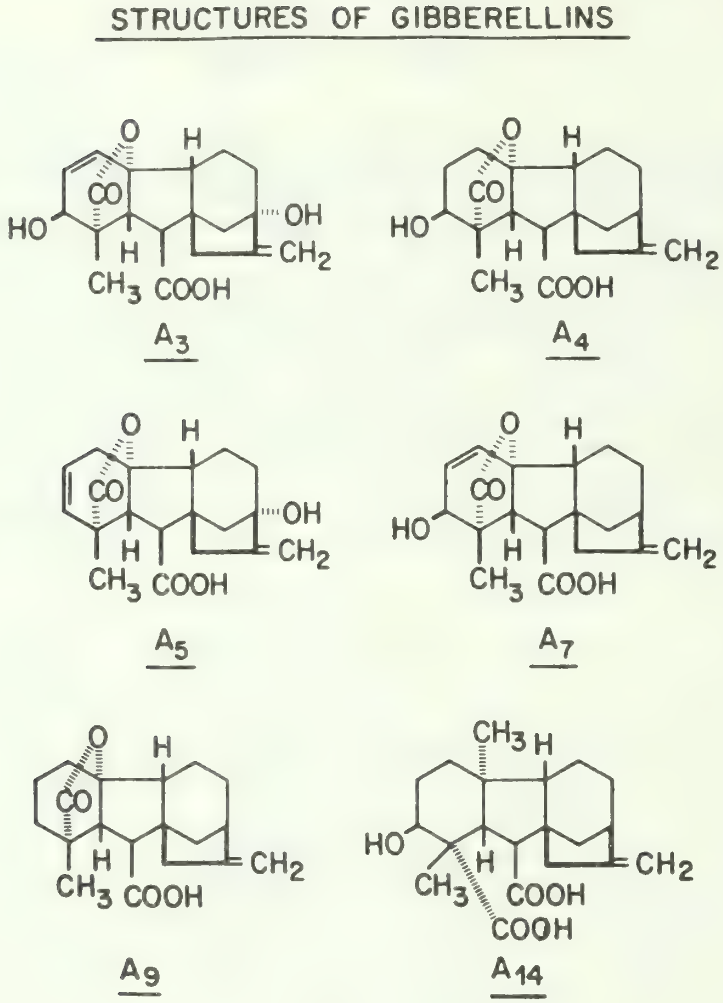

Fig. 1. Structures of 6 gibberellins (GAs) known to promote flowering in conifers. Interconversion occurs between GAs from a less-oxidized state (i.e., GA$_4$, GA$_5$, GA$_7$, GA$_9$, and GA$_{14}$) to a more oxidized state (i.e., GA$_3$) in both the fungus, (*Gibberella fujikuroi* (Saw.) Wollenw. and higher plants (see reviews by West, 1973, and MacMillan, 1974). All except GA$_{14}$ are known to be native to higher plants and GA$_3$, GA$_4$, GA$_7$, GA$_9$, and GA$_{14}$ can be produced in quantity by *G. fujikuroi*. Pathways of interconversion in the fungus are well-known, but are only now being ascertained in higher plants. Figure taken from Pharis *et al.* (1976).

frequency may vary from year to year and from clone to clone. Each species may have specific requirements with regard to type, mixture, and dosage of hormone, timing of treatment, frequency of application, and best type of additional cultural treatment.

A bit of history will also show that the hormones in question are discrete entities, not just a "class" of chemical compounds called gibberellins of which 51 are currently known (for structure, see review by Pharis and Kuo 1977).

Those of you who are not chemists or physiologists probably tend to think of auxins, cytokinins, and gibberellins as classes of hormones, individual compounds within a class having the same effect. Especially with gibberellins, this is not the case. Different gibberellins have different effects, and it is probable that plants regulate growth and differentiation by controlling the level and type of endogenous gibberellin (and other hormones).

The structures of six gibberellins known to promote flowering in conifers are shown in Fig. 1: Notice the presence or absence of the hydroxyl (-OH) group. The gibberellin that you can buy in the horticultural stores to put on your begonias is GA_3; it has two hydroxyl groups on different rings. Another gibberellin, GA_9, has no hydroxyl groups whatsoever. Gibberellins A_4 and A_7 (as a mixture) can be purchased in quantity from Plant Protection (ICI) Ltd., Fernhurt, Haslemere, Surrey, England. Gibberellin A_9 is available in small quantities only for research purposes. The other gibberellins shown are not currently available.

Gibberellins are either polar or non-polar. The polar gibberellins are those with two or more hydroxyl groups. The non-polar gibberellins have no (i.e., GA_9) or only one hydroxyl (i.e., GA_4, GA_5, or GA_7) group. Hydroxyl groups are indications of the state of oxidation. Gibberellins, as potent hormones, may be "gotten rid of" by the plant by oxidative metabolism. When you administer a gibberellin to a plant, one of its first reactions is to hydroxylate! The oxidative sequence goes from no or few hydroxyls to many hydroxyls--from a low state of oxidation to a high state of oxidation.

Secondly, the plant may begin to conjugate the gibberellins with glucose and perhaps other sugars (or sulphur, or propyl or peptidyl groups). I think that many of our past studies on gibberellins in conifers have been failures, because conifers turn out to be extremely adept in getting rid of gibberellins (c.f. ^3H-GA_4 metabolism in Douglas-fir; Wample *et al.* 1975).

Tree breeders need "sexy" trees for breeding and seed production--trees with lots of cones and lots of seeds. An example of this is shown for some ramets in a Douglas-fir seed orchard on Vancouver

Island. These grafted ramets flowered profusely; there was only one trouble, they died shortly thereafter from graft incompatibility. This profuse, or early flowering resulting from stress or trauma is a most important reaction exhibited by most woody perennial plants. It (a) gives us a tool by which we may study the physiology and biochemistry of flowering, and (b) offers us an adjunct treatment by which we may "amplify" hormone-induced flowering.

The history of gibberellins in the flowering of conifers began with the Japanese work (Y. Kato and H. Hashizume; see review by Pharis and Kuo 1977) on species of Cupressaceae and Taxodiaceae in 1956 and 1957. As examples of the high efficacy of GA_3 within these families, a seedling of Thuja plicata only 4 cm high can be made to produce staminate strobili; an ovulate strobilus was produced on a 3-month-old Sequoiadendron seedling; and for Cupressus arizonica, a 12-month-old plant sprayed with GA_3 over a period of several months, produced 8,007 strobili out of 8,090 meristems. These conifers, by the way, are nice tools for the physiologist: on just one plant there can be 8,000 to 10,000 meristems, most of which can be transformed quickly from the vegetative to reproductive state.

In addition to being "sexy" hormones, gibberellins in conifers do a lot of other things. As endogenous hormones, they affect stem elongation and diameter growth, and exogenous applications of various gibberellins will increase internode elongation, affect the apical form and apical dominance (enhance or decrease, depending upon the species), and increase diameter growth and shoot dry weight (see review by Pharis (1976a) and Pharis and Kuo (1977).

Thus, we are looking at hormones that are native to conifers, and do a lot of things besides making conifers "sexy". In fact, they appear to do most, if not all, of the vegetative growth "jobs" before doing any "reproductive work." One can perhaps generalize that gibberellins are "sexy hormones" only after they have accomplished certain vegetative growth processes; only after they build up to a certain threshold concentration do they cause sexual differentation. I propose that in the juvenile plant the gibberellins are preferentially used for vegetative purposes, sexual maturity occurring when there are enough gibberellins left over. This will generally occur on the odd meristem here and there, and only in the case of stress will a young conifer flower profusely. In each case--normal maturation, or stress-induced flowering--I propose that the flowering is caused by "left-over" endogenous gibberellins that have not been used or cannot be used for vegetative growth.

We knew from the early work of the Japanese, and from our own work, that we could readily get Cupressaceae and Taxodiaceae to flower with gibberellin A_3. We also knew that other gibberellins were effective for these two families. But Pinaceae species would not flower in response to gibberellin A_3. Furthermore, certain stress, or cultural treatments that are successful on Taxodiaceae and Cupressaceae work well in Pinaceae (see Literature Cited in Pharis (1976)), thus lending credance to a "common cause". Now, what are some of the possible reasons for this conundrum?

First, the growth habit or a meristem production habit in Cupressaceae and Taxodiaceae species is indeterminant. In other words, about every 15 to 30 days a new meristem is produced. Thus, 10 to 20 times a year each actively growing meristem has a "chance" to initiate a reproductive structure from a previously vegetative meristem (see Owens and Pharis 1967, 1972).

Thus, in the Cupressaceae and Taxodiaceae, we have access to large numbers of meristems that are continually turning over and making themselves available to possible hormonal effects resulting from exogenous hormone application. In most Pinaceae species, on the other hand, meristems can only be induced once a year, and the period of possible induction takes place during a few weeks. During these few weeks, then, its lateral primordia are trying to "decide" whether they will be lateral vegetative, lateral "latent", will abort, or whether they will become reproductive. This, then, is the time one has to hit them with the message, the hormonal signal. Perhaps many of our past experiments with hormone application missed the "differentiative" stage. In essence, an effector treatment that will induce sexual differentiation in the Pinaceae is doing so by acting upon pre-existing, undifferentiated primordia (Owens and Molder 1975), unlike Cupressaceae and Taxodiaceae whose reproductive structures are initiated from previously vegetative meristems.

In addition to the wrong timing in our experiments with Pinaceae species, we may have had the wrong gibberellin (i.e., perhaps GA_3 was a "flowering" gibberellin in Cupressaceae and Taxodiaceae, but not in Pinaceae). We therefore went back and looked at situations that would allow us to determine whether we had the right or wrong gibberellins.

We examined cultural treatments, which often (but not always), when used as the sole treatment, cause flowering. There are a number of these: starvation, nitrogen or phosphorus fertilization, girdling or strangulation, root pruning, drought stress, nitrate fertilization (in Douglas-fir, at least) are good examples. In three separate tests we applied certain of these cultural treatments to trees and then determined the endogenous gibberellins of control versus treated trees.

In Cupressus arizonica we repeated (Kuo 1973) the classic work of Lyr and Hoffman (1964), inducing both male and female flowering on Cryptomeria japonica by nitrogen starvation. In Douglas-fir, flowering can be promoted with either drought stress or calcium nitrate fertilization (Ebell 1967, 1972). On a low nitrogen site, Dr. Ebel fertilized a stand of Douglas-fir trees with calcium nitrate. Buds were sampled from treated and untreated trees, freeze-dried, extracted, analyzed for endogenous gibberellins, and the results correlated with induced flowering. Finally, Douglas-fir seedlings were subjected to drought stress.

In each experiment trees given the "flower-inducing" cultural treatment had large amounts of non-polar gibberellins compared with the controls. Conversely, the later fractions, the GA_3-like fractions and other more polar "bioassay active" fractions, were lower in trees that flowered and higher in the control trees that stayed vegetative.

So, three different cultural treatments produced similar results. Now, remember that trees that build up non-polar gibberellins are possibly trees that are not able to metabolize (i.e., hydroxylate) these non-polar gibberellins to more polar gibberellins. Thus, there may be a blockage of oxidative metabolism (or else increased synthesis over and above the ability of the tree to readily interconvert the extra quantities).

With these results in mind, we went into the seed orchards with an increased spectrum of gibberellins. We applied polar GA_3 (which we knew did not work from earlier experiments) as well as a number of the non-polar gibberellins (GA_4, GA_7, GA_9, GA_5) to grafts and seedlings of Douglas-fir and seedlings of lodgepole pine. The results were spectacular, to say the least (see appropriate figures and tables in Ross and Pharis (1976), Pharis et al. (1975), Pharis et al. (1976), Pharis 1975), Pharis and Kuo (1977)). Non-polar gibberellins, especially the $GA_{4/7}$ misture with GA_9, and a low concentration of the auxin, NAA, causes highly significant flowering--GA_3 is essentially ineffective! These earlier results have now been extended to a number of other Pinaceae species (see review by Pharis and Kuo 1977).

The strobili induced by the non-polar gibberellins can be manipulated with regard to sex. In Douglas-fir, high auxin concentrations promote male cone differentiation, low auxin increases females (just the opposite from what one would expect from work with herbaceous plants). We don't yet understand why this is the case, but for Douglas-fir, at least, work by Dr. S. D. Ross of Weyerhaeuser has confirmed this phenomenon in many experiments.

Thus, in the *Pinaceae* we have only a single period, perhaps 6 to 10 weeks, to "tell" previously undetermined buds what they are to become, whether to be male or female, vegetative, latent, or to abort. An effective treatment during this 6- to-10-week period may require that a certain threshold concentration of hormone be maintained during the entire period, and further, that photosynthate and other nutrients be readily available, not only during the 6 to 10 weeks of early differentiation, but subsequently as well. If any of these "promotive factors" is not maintained at an appropriate level, sexual differentiation ceases and abortion, or increased "latency" may occur.

Now, what about juvenility *per se*? Initially, our results were best on saplings or grafted ramets, and nil on young seedlings. Some of Dr. Ross's early work with 4-year-old seedlings showed only a non-significant" tendency" for $GA_{4/7}$ mixture to promote flowering. But, when he used cultural treatments in addition to the $GA_{4/7}$ mixture, flowering was appreciably enhanced on young seedlings.

If one wants to get young seedlings, or recalcitrant grafted clones to flower, I recommend most strongly the use of a $GA_{4/7}$ mixture with an auxin treatment and an additional cultural treatment (such as modest water stress, nitrate fertilization, or non-destructive cambial girdling). I further recommend future location of all seed orchards in warm, sunny locations (especially during early differentiation) where modest water stress in spring can be alleviated by irrigation in summer.

One of our more recent studies into just how a cultural treatment may "assist" the $GA_{4/7}$, or may cause flowering on its own, was done by Dr. A. Dunberg, at the Royal College of Forestry in Umeå, Sweden on *Picea abies*. Grafted ramets of *Picea abies* can often be made to flower by surrounding them with plastic on a light frame. Dr. Dunberg also got flowering with the non-polar gibberellins--the $GA_{4/7}$ and GA_9 treatment being most effective. Thus, as with Douglas-fir, a non-hormonal "flower-inducing" cultural treatment existed for *P. abies*, and *P. abies* also responded to treatment with non-polar gibberellins.

Trees surrounded by plastic were given a radioactive gibberellin (3H-GA_4) of very high specific activity (i.e., the actual amount of GA_4 was so low as to be metabolized by the tree as if it were a "native" gibberellin). The GA_4 was not enough for the tree to "see" physiologically, but was radioactive enough for us to see in terms of how the tree metabolized it. After 48 to 96 hours of incubation in the field, extracts of control and "plastic-treated" branches were made and analyzed by gas chromatography-radiochromatogram scanning. Under conditions that cause flowering (i.e., plastic on frames), metabolism of 3H-GA_4 to more polar gibberellins was depressed, relative to metabolism in control branches. Thus, a cultural treatment that causes flowering, results in a build-up of the non-polar GA_4, relative to non-flowering control branches--a situation analogous to the work on endogenous gibberellins of Doulas-fir and Cupressus arizonica given flowering promotive cultural treatments!

Some other examples of flowering promotion in Pinaceae species are as follows:

Pinus contorta grafted ramets. The $GA_{4/7}$ mixture dripped onto the bud; Prince George, B.C., N. Wheeler, B.C. Forest Service, Research Division. For the treated terminal shoot, frequency of flowering: control-33%; low $GA_{4/7}$--54%; high $GA_{4/7}$--42%. Notice, the supraoptimal effect of $GA_{4/7}$. If we look at the number of females: 0.67--control; 1.79--low $GA_{4/7}$; 1.17--high $GA_{4/7}$. Again, the supraoptimal effect. But, if we look now at females on lateral branches adjacent to the treated shoots: control--17%; low $GA_{4/7}$--21%, high $GA_{4/7}$--25. If we look at number of females on adjacent lateral branches: 0.17--control; 0.71--low $GA_{4/7}$; 0.67--high $GA_{4/7}$. If we look at all other branches on the ramets, flowering frequency is control--25%; low $GA_{4/7}$--29%; high $GA_{4/7}$--38%. Number of flowers for "all other branches" of the ramet: 1.08--control; 1.04--low $GA_{4/7}$; 1.54-$GA_{4/7}$. And, if for this experiment we pull a "sexy" clone out; (SK5) clone comes out: For treated terminals, control--11%, low $GA_{4/7}$--27%, high $GA_{4/7}$--37%; for number of females on the terminals, control--0.18, low $GA_{4/7}$--0.55, high $GA_{4/7}$--0.82.

Picea glauca grafted ramets. Work by G. Kiss, B.C. Forest Service, Research Division, Prince George, B.C. shows a female flowering frequency of: control--0 out of 48; low $GA_{4/7}$--7 out of 48 females; high $GA_{4/7}$--5 out of 48. For number of female strobili (total): control--0.0; low $GA_{4/7}$--15.0; high $GA_{4/7}$--14.0. But, because of the adjunct girdling treatment many branches were lost to snow breakage. For example, control without girdling--0 of 48 branches lost; control with girdling--15 out of 48; low $GA_{4/7}$--15 out of 48; high $GA_{4/7}$--21 out of 48 branches lost. However, although we lost almost half of the branches in the high $GA_{4/7}$ treatment, we still got reasonable flowering (i.e., 14 females).

Similarly good results on P. glauca were obtained by R. M. Rauter (using GA_4 on grafted ramets) in both 1976 and 1977, and in an experiment on 55-year-old P. glauca trees. $GA_{4/7}$ plus auxin plus girdling proved to be an effective treatment, control flowering being essentially zero.

In summary, flowering promotion in many Pinaceae species is now a reality, using certain of the non-polar gibberellins, especially in admixture, and with an auxin and adjunct "cultural"treatments. However, each species, each age, each clone, and each site (i.e., geographic location) may have to have highly "specific" treatments (in terms of dosage level, frequency of application, hormone mixtures, and adjunct cultural treatments) developed to insure success. Results thus far lead me to strongly recommend the "hormonal" approach for the breeder, but it is still too early to make such a recommendation to the seed orchard manager--much additional research work is required in this latter area.

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LONGLEAF PINE FLOWERING IN RESPONSE TO NITROGEN FERTILIZATION, BRANCH GIRDLING, GROWTH SUBSTANCES, AND CULTIVATION

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ABSTRACT.--Biweekly applications of 400 μg $GA_{4/7}$ plus 25 μg NAA per bud from June 1 to August 10 promoted male and female flowering in longleaf pine (*Pinus palustris* Mill.), especially when combined with partial branch girdling and NH_4NO_3 fertilization. Fertilization was the most effective single factor, and girdling was second. Cultivation had no significant effect on flowering. Vegetative bud growth was doubled by GA-NAA, independent of fertilizer stimulation.

Poor pollen production has seriously hindered improvement breeding in longleaf pine. Certain cultural treatments (nitrogen fertilization, cultivation, subsoiling) and branch treatments (partial girdling, gibberellins) increase flowering in conifers. Varnell (1970) found that partial branch girdling increased eightfold the number of longleaf pine branch tips bearing male flowers, but did not increase female flowering. With loblolly pine (*P. taeda* L.) nitrogen fertilization promotes female flowering (Schmidtling 1974, van Buijtenen 1966). However, van Buijtenen reported that this was accompanied by a decrease in male flowering, and he also found that cultivation increased both male and female flowering.

Gibberellins (GAs) have enhanced flowering in many conifers (Pharis 1974, 1975, 1976). GA_3 is effective except in Pinaceae species, which require a less polar gibberellin like $GA_{4/7}$. Biweekly bud applications of 400 μg $GA_{4/7}$ combined with partial branch girdling promoted flowering in loblolly pine. Low levels of naphthaleneacetic acid (NAA) combined with $GA_{4/7}$ further improved flowering.

Our experiment tested effects of partial branch girdling, GA-NAA bud application, NH_4NO_3 fertilization, and shallow cultivation on the percentage of buds with male and female flowers. An attempt was also made to evaluate the effects of these treatments on the number of flowers per flowering bud.

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MATERIALS AND METHODS

Twenty 13-year-old longleaf pines with poor flowering histories were selected from a thinned south Mississippi plantation which was beginning to flower. Average diameter at breast height was 18 cm.

Four cultural treatments (control, fertilized, disked, and fertilized plus disked) were randomly assigned in each of five blocks containing four trees each. In late May, 900 g NH_4NO_3 were distributed evenly among six 30 cm deep holes around the drip lines of the designated trees. Trees selected for soil treatments were far enough apart to avoid cross-over effects. Light disking beneath the crown was done in late May.

Eight branches were selected on each tree--four in the lower crown and four in the mid- to upper crown (hereafter called upper). Four branch treatments (control, partial girdle, GA-NAA, and partial girdle plus GA-NAA) were randomly assigned at each crown level. Branches were girdled in late May 1976 by removing two staggered strips of bark and cambium. Strips were 1 cm apart, 1 cm wide, and covered 3/4 of the branch circumference. From June 1 to August 10 growth substances were applied biweekly to each bud in dosages of 400 µg $GA_{4/7}$ and 25 µg NAA in 0.1 ml 50% ethanol.

In February 1977, each bud was measured for length, and male and female flowers were counted. Data were then calculated on a branch basis for average bud length, percentage of buds with male flowers, percentage with female flowers, and average number of male and female flowers per flowering bud.

The statistical design was a split-split plot with five replicates: whole plots were soil treatments, first order subplots were crown levels, second order subplots were branch treatments. Analysis of variance was used to test for significance at the 0.05 level of probability.

RESULTS AND DISCUSSION

Bud length increased with nitrogen fertilization and doubled with GA-NAA treatments (fig. 1). Disking had no effect and girdling reduced bud growth. Girdling plus GA-NAA increased bud length less than did GA-NAA alone. For bud growth, there were no significant soil/branch or soil/crown level interactions. Upper crown buds averaged more growth than lower crown buds.

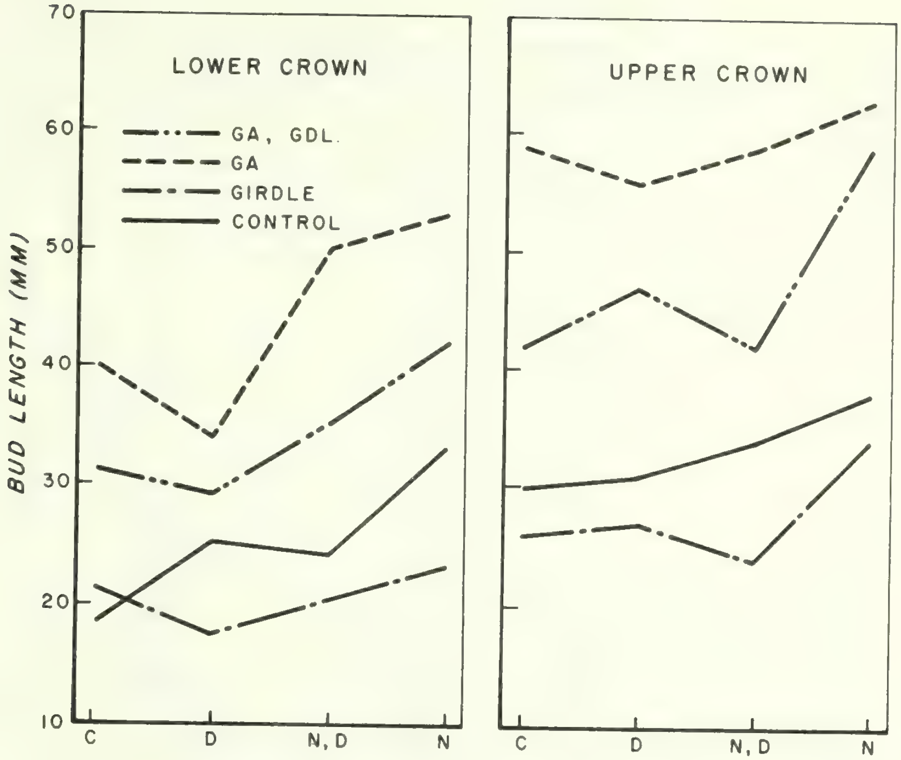

Figure 1.--Effect of soil and branch treatments on average bud length. Soil treatments were control (C), disking (D), NH_4NO_3 fertilization plus disking (N,D), and NH_4NO_3 fertilization alone (N). Branch treatments were control, girdle, $GA_{4/7}$ - NAA (GA), and girdle plus $GA_{4/7}$-NAA (GA,GDL).

Nitrogen generally promoted both male and female flowering, but there was no significant effect from disking nor nitrogen plus disking (figs. 2 and 3). In fact, the combination of disking and nitrogen usually produced fewer flowers than either treatment alone.

All three branch treatments promoted flowering. At both crown levels female flowering was promoted best by GA-NAA plus girdle (fig. 2). Combined with nitrogen fertilization this treatment gave 50% female flowering in the upper crown, compared with no flowering on the control. For male flowering in the upper crown the combined branch treatment was less effective than girdling alone (fig. 3), which produced 60% flowering on fertilized trees. In the lower crown the three branch treatments were about equally effective for male flowering.

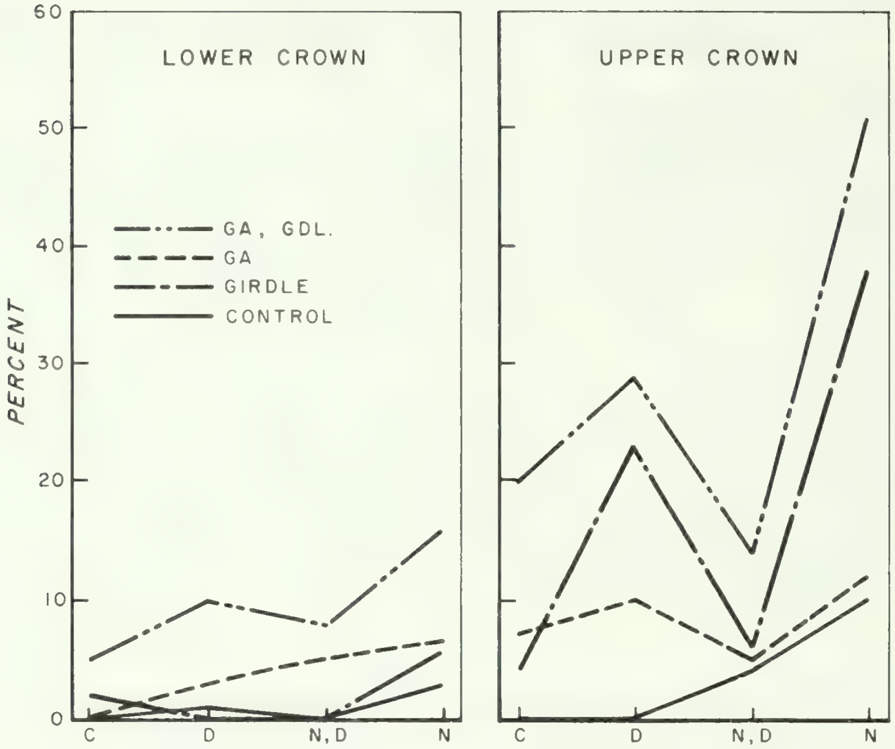

Figure 2.--Effect of soil and branch treatments on percentage of buds with female flowers. Soil treatments were control (C), disking (D), NH_4NO_3 fertilization plus disking (N,D), and NH_4NO_3 fertilization alone (N). Branch treatments were control, girdle, $GA_{4/7}$-NAA (GA), and girdle plus $GA_{4/7}$-NAA (GA, GDL).

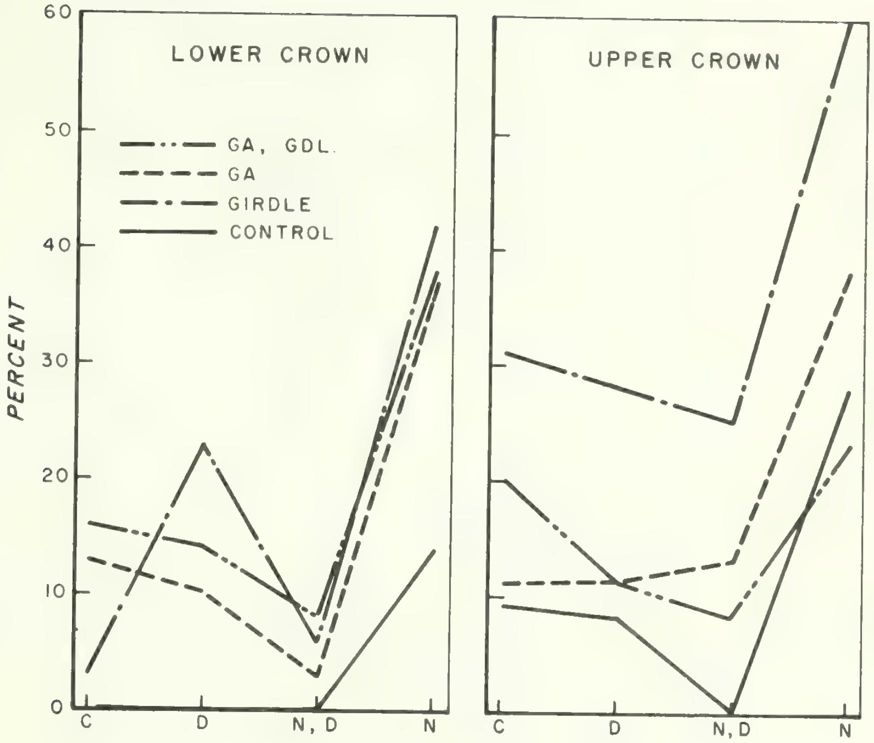

Figure 3.--Effect of soil and branch treatments on percentage of buds with male flowers. Soil treatments were control (C), disking (D), NH_4NO_3 fertilization plus disking (N,D), and NH_4NO_3 fertilization alone (N). Branch treatments were control, girdle, $GA_{4/7}$-NAA (GA), and girdle plus $GA_{4/7}$-NAA (GA,GDL).

Most of the literature on promoting pine flowering deals only with the percentage of branch tips having male or female flowers. More important is the total flower production, which depends not only on percentage of flowering buds but also on number of flowers per flowering bud. Unfortunately, treatment effects on flowers per flowering bud in this study could not be compared statistically because some branches had no flowers. It appeared, however, that branch treatments increased flowering percentage but decreased the average number of flowers per flowering bud, whereas nitrogen fertilization markedly increased both male and female flowering percentage and number of flowers per flowering bud. These observations might be explained if nitrogen is a limiting factor in flower initiation and development. Induction of more flowering buds by branch treatments may channel nitrogen for amino acid synthesis into these new sinks, thus limiting substrate per bud and allowing fewer flowers to form. Girdling may induce more buds to flower by keeping organic nitrogen compounds and carbohydrates from moving out of the branch via the phloem, but without nitrogen fertilization the number of flowers produced will be limited.

From this experiment we conclude that a combination of NH_4NO_3 fertilization, partial branch girdling, and bud treatment with $GA_{4/7}$ plus NAA most effectively promotes longleaf pine flowering. Cultivation is ineffective or even detrimental with fertilization. At present only fertilization appears to lend itself to an operational program in seed orchards. Girdling takes too much time and occasionally kills the branch. If GA-NAA could be applied by foliar spray the treatment would be practical, but GA appears to require tedious application to individual buds (Pharis et al.1975).

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EFFICIENCY OF SEED PRODUCTION IN SOUTHERN PINE SEED ORCHARDS

David L. Bramlett[1]

ABSTRACT.--Seed production in southern pine seed orchards can be evaluated by estimating the efficiency of four separate stages of cone, seed, and seedling development. Calculated values are: cone efficiency (CE), the ratio of mature cones to the initial flower crop; seed efficiency (SE), the ratio of filled seeds per cone to the seed potential; extraction efficiency (EE), the ratio of extracted seeds per cone to the total seeds; and germination efficiency (GE), the ratio of germinated seeds per cone to the filled seeds. The product of these four efficiency values is the overall seed orchard to nursery efficiency (SO-NE). With SO-NE, the orchard manager can compare the actual yield of seedlings produced from the orchard to the maximum biological potential of a given flower crop to produce viable seeds. The two approaches to increasing production of seed orchards are to increase flower production and to increase CE, SE, EE, or GE values. Computation of efficiency values pinpoints major types of seed losses and shows where corrective actions should be concentrated.

The tree improvement program in the South now has many thousand acres of established pine seed orchards. The seeds from these orchards contain the improved growth, wood quality, and pest resistance of a new generation of forest trees. To economically meet the demand for these seeds, it is important that each orchard produce seeds efficiently.

The reproductive process begins with initiation of flower primordia and ends with seedlings. In this paper, however, I discuss only the development and maturity of seed after the flowers have been formed. The primary stages of seed orchard production discussed are cone development, seed yield per cone, extraction of mature seeds, and germination of filled seeds.

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CONE DEVELOPMENT

Survival and normal development of a high percentage of cones is critical because loss of a cone means loss of its entire set of seeds. For a given flower crop in the seed orchard, cone development can be evaluated in terms of cone efficiency. This value is the ratio of the harvested cones to the original flower crop.

$$\text{Cone efficiency} = \frac{\text{Number of harvested cones}}{\text{Number of female flowers initiated}} \times 100\%.$$

The calculated cone efficiency value gives the overall survival of a flower crop but it does not identify specific causes of cone mortality. In shortleaf pine (*Pinus echinata* Mill.) studies in Virginia, the majority of mortality occurred during the spring and summer following pollination. The average cone efficiency for flower crops from 1963-1969 was 29 percent; 61 percent of the potential cone crop was lost in the first year and only 10 percent lost in the second year (Bramlett 1972). To evaluate seasonal losses, a periodic count is necessary. The Georgia Forestry Commission Seed Orchard has utilized a subsample of 10 tagged branches on randomly chosen sample trees. The cones on the tagged branches were counted a total of 10 times during the cone developmental period and flower and clone mortality were recorded (Godbee and others 1977). DeBarr and Barber (1975) charted the development of a flower crop and identified specific causes of cone mortality on life tables.

Since cone efficiency is the percent survival of an initial flower crop, the actual number of original flowers strongly influences cone efficiency. With a constant cone efficiency a greater number of flowers are lost as the size of the flower crop increases. Conversely, if the number of cones lost in each flower crop remains constant, then the cone efficiency decreases for small flower crops and increases for large flower crops. A further complication occurs when the previous cone crop influences the succeeding crop in terms of increasing mortality the year following a year with abundant flowering. This increase apparently is the result of an increase in insect populations from the preceding year. For example, cone efficiency of a natural stand of shortleaf pine was only 3 percent in 1964 as a result of a severe spring frost in 1963. The following year a large flower crop was produced with a correspondingly high cone efficiency of 65 percent. The flower production remained relatively high for the next two years, 1966 and 1967, but mortality in numbers of cones increased annually and the cone efficiency likewise decreased. Flower production was again low in 1968 but cone efficiency remained at 25 percent. Flower production increased to its highest level in 1969 and the projected cone crop (based on first-year survival) would give a cone efficiency of approximately 48 percent.

SEED YIELD PER CONE

Once the cones are mature and harvested, the seed yield per cone can be measured and compared to the capacity of the cone to produce seeds. Each pine cone contains a series of scales spirally arranged on a central axis. The cone scales can be counted and classified as fertile or infertile in a cone analysis technique developed by Bramlett and others (1977). Average values for total number of scales on sampled cones from 4 southern pines were 87 for shortleaf, 111 for Virginia (P. virginiana Mill.), 135 for loblolly (P. taeda L.), and 149 for slash pine (P. elliottii Engelm.) (Bramlett 1974). The total number of scales per cone, however, is not an accurate measure of the capacity of the cone to produce seeds. To quantify the seed production capacity, only the fertile or seed bearing scales should be counted (Lyons 1956). The fertile scales occur in the upper one-half to two-thirds of the cone and are distinguished from the lower, infertile scales by the presence of functional ovules or seeds. Also, fertile scales are wider at the base and in general larger than infertile scales.

Each fertile scale is capable of producing two seeds. Thus, for each cone, seed potential is:

$$\text{Seed potential} = 2 \times \text{number of fertile scales.}$$

Seed potential is the maximum number of seeds that the cone is biologically capable of producing. The seed potential observed in sample cones averaged 170 for slash pine, 155 for loblolly pine, 88 for Virginia pine, and 87 for shortleaf pine (Bramlett 1974).

Although the seed potential establishes the upper biological boundary for seed production from a given cone, the actual yield of filled seeds is the only product of value from the orchard. Seed efficiency is determined by comparing the yield of filled seeds per cone with the seed potential for that cone.

$$\text{Seed efficiency} = \frac{\text{Number of filled seed}}{\text{Seed potential}} \times 100\%.$$

Seed efficiency can be used to evaluate the seed performance of a given tree, clone, or seed orchard. For example, a sample of slash pine cones in 1972 yielded 28 filled seeds per cone. Since the seed potential was 170 seeds, the seed efficiency was 28/170 = 16 percent. Comparable values for loblolly, Virginia, and shortleaf pine were 24 percent, 19 percent, and 14 percent for the samples evaluated.

SEED LOSSES

Seed efficiency values ranging from 14 to 24 percent seemed disappointing, and it was important to examine the causes of seed failure in the remaining 86 to 76 percent of the potential seeds. The cone analysis procedure was used to place all ovulates and seeds on the extracted cone scales into four classes: (1) First-year aborted ovules, (2) second-year aborted ovules, (3) empty seed, and (4) filled seed. After the losses in each class were estimated, specific causes of seed losses were sought.

First-year aborted ovules.--First-year aborted ovules are potential seeds that abort during the first growing season. In mature cones, therefore, they are no larger than normal ovules after one year of development. The wing develops normally, however, and these ovules are "wings without seeds."

First-year abortion of ovules was a major type of loss in slash pine and loblolly pine. In 1972 sample cones, slash pine lost 110 seeds per cone and loblolly pine lost 69 seeds as first-year aborted ovules. These losses represented 65 percent and 44 percent of the seed potential for these two species.

The high losses in this category made it very important to identify specific causes. Two causes were known: Pollination failure (Sarvas 1962, McWilliam 1959), and feeding by seedbugs, particularly Leptoglossus corculus (DeBarr and Ebel 1973). The early instars of this insect are able to penetrate the conelet, puncture the integument and extract large portions of the ovule. Feeding damage of this type can be identified macroscopically and confirmed by microscopic examination (Bramlett and Johnson 1975). When feeding of seedbug occurs for an extended period, the conelet may also abort (DeBarr and Kormanik 1975).

In addition to these established causes of first-year ovule abortion, other causes are suspected. Apparently, for unknown reasons, some pollinated ovules do not develop. Also, fungi may cause ovule deterioration (Miller and Bramlett 1975), but specific details are not yet established.

Second-year aborted ovules.--Second-year aborted ovules survive the first year of development but abort during the second year before the seedcoat is well formed. These ovules appear resinous, collapsed, or necrotic in early summer. Frequently, resin streaks are also visible in the vascular cells of the scale. In addition to the large necrotic ovules, some aborted ovules produce a small seed coat but are not as large as a fully developed seed.

Heavy losses of this type were observed on shortleaf and Virginia pines. Shortleaf pine averaged 41 second-year aborted ovules per cone (47 percent) and Virginia pine had 31 (36 percent) in samples from unprotected natural stands. Sample cones of loblolly and slash pine had 23 and 17 second-year aborted ovules per cone or 15 percent and 10 percent of the seed potential.

The major cause of second-year aborted ovules in pines is feeding by pine seedbugs on the developing cones. Krugman and Koerber (1969) described feeding damage of *Leptoglossus occidentalis* on ponderosa pine (*P. ponderosa* Laws.). DeBarr (1967) identified two seedbugs that damage southern pine seed. DeBarr and Ebel (1974) increased seed yield in shortleaf and loblolly pine with screen cages and described ovule damage associated with feeding of *Leptoglossus corculus*. Bramlett and Moyer (1973) were able to eliminate almost all second-year aborted ovules in Virginia pine with protective screen wire cages that excluded seedbugs prevalent in the area.

These observations show that seedbug damage is responsible for most second-year abortion of ovules. The cause of the smaller, hardened, aborted ovules is not known. Some preliminary indications associated this type damage with moisture or nutritional stress during development.

Empty seeds.--All seeds have some remnants of gametophyte tissue and/or a shriveled or damaged embryo. They were formerly classed as empty if they would float in 95 percent ethanol, and they are now usually recognized by X-ray detection. In a broad sense, seeds damaged by seedbugs or fungi, and seeds with abnormal development can be grouped as empty seeds.

In a well-managed seed orchard, 85 percent of the seeds should be filled. In the absence of protection from insects, values below 50 percent have been observed. Known causes of empty seeds include insects, fungi, and embryonic lethal alleles.

Insect attack and damage seed in the nearly mature or mature cone. Unlike cone-destroying insects such as *Dioryctria* spp., the leaf-footed pine seedbug and the shieldback seedbug feed on seeds without leaving external signs of damage on the cone. External damage on the seedcoat may also be minimal, even when the embryo is killed (DeBarr 1970).

Insects are not the only cause of empty seeds in pines. Even when protective screen cages are used to exclude seed insects, empty seeds are found in the sample cones (Bramlett and Moyer 1973; DeBarr and others 1975; DeBarr and Ebel 1973). Many studies have shown an increase in the percentage of empty seeds following self-pollination (Franklin 1970). These empty seeds are the result of recessive embryonic lethal alleles that cause embryo mortality soon after fertilization. Although pines may have polyzygotic embryony, selfing and other forms of inbreeding increase the probability of embryo abortion in the pine ovule. Empty seeds are the result (Bramlett and Popham 1971). Empty seeds also occur following cross pollinations or wind pollinations. Embryo mortality following cross pollinations (with screen cage protection) are apparently due to the random matching of the recessive embryonic lethals (Bramlett and Pepper 1974).

Other classes of seed loss or damage include seedworm (Laspeyresia spp.) damage, abnormality, fungal infection, and incompletely filled seeds. The cumulative total of these seed losses is usually less than 10 percent and normally is not a serious problem in the seed orchard.

Filled seeds.--Filled seeds have the potential to germinate; they have healthy, undamaged gametophyte tissue, a normal embryo, and no evidence of fungi or other destructive pests. They are the end product of the seed orchard and represents the final yield from an initial crop of female flowers. As previously stated, the ratio of filled seed to the seed potential gives the seed efficiency per cone. Seed orchard efficiency is calculated by combining seed efficiency and cone efficiency.

$$\text{Seed orchard efficiency} = \frac{\text{Cone}}{\text{Flowers}} \text{ X } \frac{\text{Filled seed}}{\text{Seed potential}} \text{ X } 100\%$$

$$= \text{Cone efficiency X Seed efficiency X } 100\%.$$

Seed orchard efficiency can be used to evaluate seed orchard performance. For example, an initial crop of 8,000 flowers per acre in a slash pine seed orchard would have a biological potential of 8,000 X 170 (seed potential) for slash pine or 1,360,000 seeds. Based on an average of 13,500 cleaned seeds per pound for slash pine, this yield would equal ca 100 pounds of seeds per acre. The fate of these seeds is determined by the amount of loss occurring during the development period. For example, under intensive management approximately 75 percent of the initial flowers could become mature cones. Losses would include not only insect damage, but other abiotic factors such as unharvested cones, wind damage, trees lost to lightning, etc. With a 75 percent cone efficiency and a similar 75 percent seed efficiency, the orchard would produce 56 percent of the biological potential, or 56 pounds of seeds per acre. This value may represent the upper limit that can be expected in seed orchards even under excellent management.

Under typical management, a seed orchard may produce 50 percent cone and seed efficiencies, but since seed orchard efficiency is the product of these two values, the overall efficiency is only 25 percent. Under poor or no management, seed efficiency may be below 10 percent. Cone efficiency X seed efficiency in a natural stand of shortleaf pine ranged from 0.5 to 17.4 percent during 5 years of observations and averaged about 4 percent (Bramlett 1972).

SEED EXTRACTION

The percentage of seed removed by extraction can be important to the overall seed efficiency. The primary factor is the degree of cone opening after heating in the extraction kiln. Poor cone opening may be associated with cones harvested too early, fungal damage, insect damage, or case hardening during storage. These causes combined represent a net loss of seeds supplied to the nursery. The quantity of seeds lost during the extraction process can be estimated by comparing number of seeds extracted to the total number produced by the cone. This value is the extraction efficiency.

$$\text{Extraction efficiency} = \frac{\text{Number of seeds extracted}}{\text{Total number of seeds/cone}} \text{ X } 100\%.$$

SEED GERMINATION

When a seed germinates and produces a seedling, the final link between generations is complete. Germination is the subject of considerable literature but for this paper will simply be considered as the percentage of filled seeds that germinate normally during a specified test period. Germination efficiency (percent germinated) is determined for each cone.

$$\text{Germination efficiency} = \frac{\text{Number of germinated filled seeds}}{\text{Total number of filled seeds}} \text{ X } 100\%.$$

Germination of a pine seedlot is normally between 70 and 90 percent. The average germination efficiency value can be combined with previous efficiency values to estimate overall seed orchard to nursery efficiency.

SEED ORCHARD TO NURSERY EFFICIENCY

The ability of a seed orchard to produce not only seeds but seedlings can be evaluated as a product of the four separate efficiency statements, cone efficiency (CE), seed efficiency (SE), extraction efficiency (EE), and germination efficiency (GE). Thus, seed orchard-nursery efficiency (SO-NE) is:

$$\text{SO-NE} = \text{CE} \times \text{SE} \times \text{EE} \times \text{GE}.$$

Using this combined efficiency value, the seed orchard manager can evaluate the overall performance of a given flower crop to produce seedlings for the nursery. With excellent seed orchard management and protection, efficiency values of 75 percent are possible for CE and SE and 90 percent for EE and GE. Thus, SO-NE = 0.75 x 0.75 x 0.90 x 0.90 = 0.45. This value of 45 percent efficiency may approach the upper biological limit for an operational seed orchard. Levels of SO-NE below 45 percent indicate that some improvements may be possible.

Godbee and others (1977) used SO-NE to evaluate an insecticide spray program in a Georgia Forestry Commission seed orchard. The SO-NE averaged 17 percent on plots treated with the insecticide, compared to 6 percent in the control plots. This evaluation indicated that the spray program was increasing the seeds and seedlings produced in the orchard, yet substantial losses were still occurring. Modifications in the insect control program have now been implemented to provide more effective control.

Evaluation of seed orchard performance by computing efficiency values suggests two general ways to increase the seed production of seed orchards. The first is to increase flower production while holding values for CE, SE, EE, and GE constant. The second is to reduce seed losses during one or more of the developmental stages. The logical approach to reduce seed losses is to first evaluate seed production efficiency and identify and quantify the specific causes of seed losses. Once the seed losses are known, control measures can be prescribed to prevent or reduce the losses. If the orchard manager knows the impact of a specific loss and the cost of the control, he can evaluate the projected increase in seed efficiency and seed yield.

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FLOWER PRODUCTION ON CLONAL ORCHARDS AT OCONTO RIVER SEED ORCHARD IN WISCONSIN

J. G. Murphy and R. G. Miller[1]

ABSTRACT.--The Eastern Region, USDA Forest Service has been establishing and managing seed orchards to produce improved seed for the National Forests in the Lake States since 1969. This paper presents a review of the female flower production for the past 4 years in the white pine, white spruce, and black spruce clonal seed orchards.

The tree improvement program being conducted on the National Forests in the Lake States has been described in detail (Miller and Murphy 1976). The Lake States National Forests have been divided into nine seed collection zones and four breeding zones (fig. 1). Beginning in 1969, seed orchards were established by breeding zone for selected species at the Oconto River Seed Orchard complex located near Langlade, Wisconsin. The number of ramets required to produce anticipated seed needs in the various orchards were based on research information (Nienstaedt and Jeffers 1970) and best estimates of potential production. Information on cone production, frequency of crops, and flowering of individual clones is needed to make better estimates of potential cone production in large scale seed orchards for white spruce, black spruce, and white pine. Female flower data collected between 1973 and 1977 will be reported for two white pine, four white spruce, and two black spruce clonal seed orchards.

SEED ORCHARDS

Following is a brief description of the plant materials included in the seed orchards (table 1).

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Table 1.--Individual seed orchard statistics

Species	Orchard no.	Breeding zone[1/]	Clones	Grafts	Acres	Year of establishment	Year of first flowering
			- - -	Number	- - -		
White pine	1	All	798	3,612	40	1969	1973
White pine	3	All	36	830	10	1969	1973
White spruce	4	A	56	903	21	1969	1974
White spruce	6	B	50	1,128	21	1969	1974
White spruce	14	C	40	1,128	14	1973	1974
White spruce	16	All	39	220	5	1973	1974
Black spruce	8	A	50	1,501	21	1971	1974
Black spruce	10	B	47	778	20	1973	1974

[1/] Breeding zones are shown in figure 1.

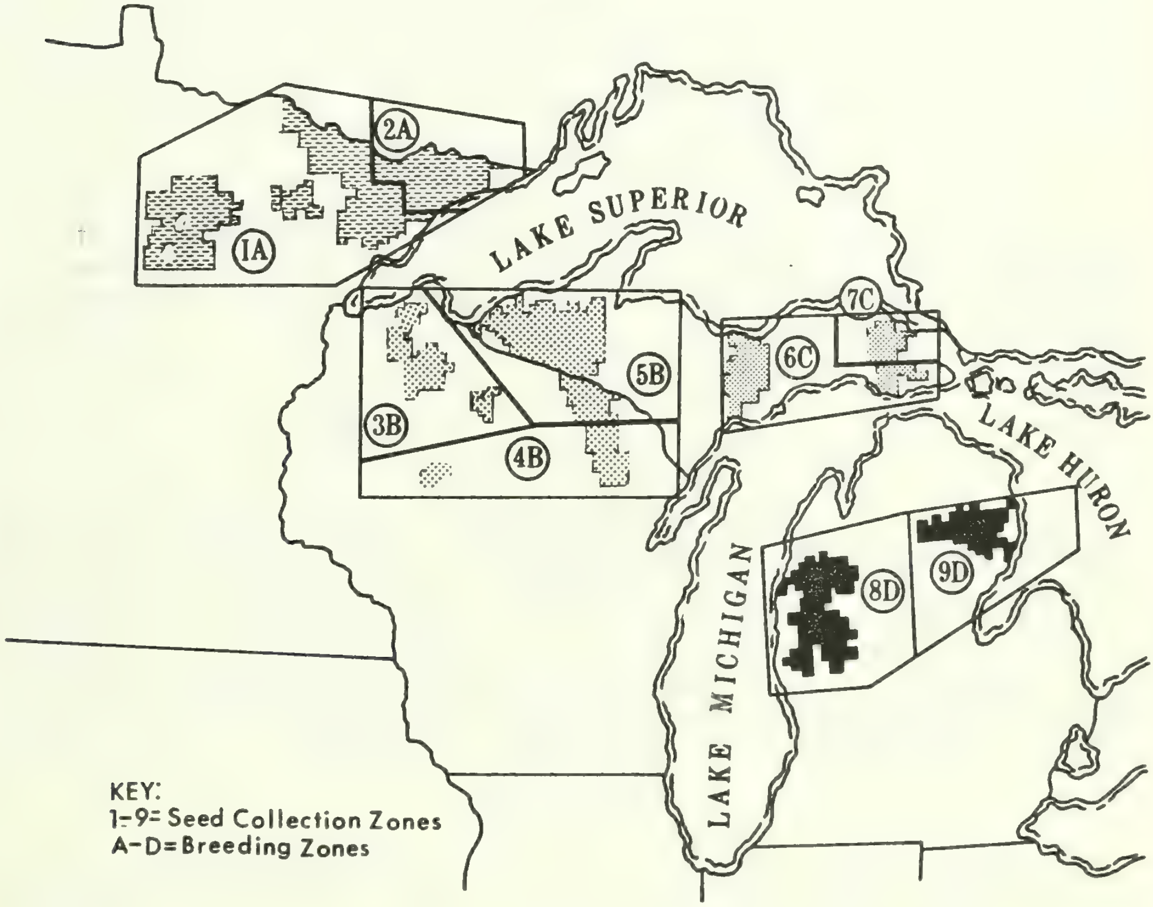

Figure 1.--Seed collection zones and breeding zones.

White Pine Orchards 1 and 3

Orchard 1 (white pine breeding arboretum) contains ramets from 798 ortets selected for their apparent resistance to white pine blister rust. The majority of the ortets came from the Lake States; however, a few came from Eastern States.

Orchard 3, which is an interim seed orchard, contains five clones selected by Drs. Riker and Patton, University of Wisconsin, and 31 clones selected by Drs. Heimburger and Zsuffa, Maple, Ontario, Canada. The majority of orchard 3 was established in 1969 whereas orchard 1 was established over a 5 year period.

White Spruce Orchards 4, 6, 14, and 16

The plants in orchards 4, 6, and 14 were selected on National Forests in breeding zones A, B, and C, respectively. The material in orchard 16 was selected by personnel of the North Central Forest Experiment Station in Rhinelander, Wisconsin, from ortets originating from seed collected in the Ottawa River Valley in Ontario, Canada, and growing in provenance tests. All of the white spruce orchards have had ramets added each year since the original planting. Orchard 4 suffered large losses following the second year planting, resulting in much more age variation than the other white spruce orchards.

Black Spruce Orchards 8 and 10

Plant materials in orchards 8 and 10 were selected on National Forests in breeding zones A and B, respectively. Both of the black spruce orchards have had ramets added each year since the original planting.

DATA

Collection

The flowering data for white pine and white spruce were collected in the spring as part of the breeding program. The black spruce flowering data were determined by cone collections in the fall with the possibility of some flowers being lost due to frost. All flower data are recorded as 1: none, 2: female, 3: male, and 4:male and female for each ramet and then summarized using the Region 9 tree improvement computer programs. The data do not account for the quantity of flowers produced, but only whether a ramet has produced one or more flowers.

Computation

The number of living trees and number of clones represented in all the orchards varies from year to year because the orchards were established over a period of time. Therefore, the data were converted to percent of trees and percent of clones that produced female flowers. The data represent the following years: white pine, 1973-1976 (table 2); white spruce, 1974-1977 (table 3); and black spruce, 1974-1976 (table 4). The frequency of clones producing flowers during the data collection period was calculated for orchards 3, 4, and 6 (table 5).

Table 2.--Living ramets and clones with female flowers for white pine

(In percent)

Orchard no.	Type of material	Year			
		1973	1974	1975	1976
1	Ramets	19	18	4	4
	Clones	36	34	10	11
3	Ramets	21	31	18	6
	Clones	69	83	69	39

Table 3.--Living ramets and clones with female flowers for white spruce

(In percent)

Orchard no.	Type of material	Year			
		1974	1975	1976	1977
4	Ramets	24	17	12	33
	Clones	79	46	39	92
6	Ramets	20	19	9	75
	Clones	85	82	60	100
14	Ramets	71	20	16	55
	Clones	91	89	80	98
16	Ramets	34	8	5	44
	Clones	64	41	21	66

Table 4.--Living ramets and clones with female flowers for black spruce

(In percent)

Orchard no.	Type of material	Year		
		1974	1975	1976
8	Ramets	(No data)	28	29
	Clones	(No data)	94	90
10	Ramets	41	33	21
	Clones	92	74	89

Table 5.--The frequency of clones producing flowers over a 4-year period

(In percent)

Seed orchard and	species	Number of years out of four				
		4	3	2	1	0
3	White pine	30	39	6	11	14
4	White spruce	29	23	34	9	5
6	White spruce	46	42	8	4	0

Correlation coefficients were computed between percent of living trees with flowers and ortet age for orchards 4 and 6 (table 6).

Table 6.--Correlation coefficient of percent of living trees with flowers and ortet age[1]

Orchard no.	Year		
	1974	1975	1976
4	+.04	-.22	-.25
6	+.24	+.16	+.28

[1] Not significant at the 95 percent level.

For the data available for each orchard, correlations were computed between a month's total rainfall by year and the following year's percent of ramets producing flowers. This was done for the months May through September (table 7).

Table 7.--Correlation coefficient of percent of living ramets with flowers and the previous years rainfall by months

Species and flower data year	Orchard no.	Month: May	June	July	Aug.	Sept.
White pine	1	+.23	-.96[1]	+.64	+.28	-.08
(1973-1976)	3	+.67	-.73	+.40	-.09	-.70
White spruce	4	+.24	-.81	-.56	-.82	-.86
(1974-1977)	6	-.19	-.48	-.78	-.72	-.73
	14	+.77	-.97[1]	-.17	-.80	-.62
	16	+.41	-.88	-.53	-.91	-.76
Black spruce (1974-1976)	10	+.91	-.95[1]	+.78	-.40	-.91

[1] Significant at the 95 percent level.

DISCUSSION

The flowering trend for the eight seed orchards between 1973/74 and 1976 shows a decline in the number of ramets and number of clones that produced flowers. The decline may be due to normal cyclic production. A review of the amount of seed produced from the flowering years indicated similar results. In all four of the white spruce orchards a total of 3.00 lbs. of seed was produced in 1974, 0.25 pounds in 1975, and 0.002 pounds in 1976. However, 1977 was the best flowering year to date in the white spruce orchards. Data on white pine and black spruce for 1977 flowering have not been tabulated, but observations indicate that flowering is good in these orchards as well.

A review of the computer data summaries for each of the orchards revealed a large amount of variation among clones in year-to-year production. Many clones produce consistently but a few clones never have and maybe never will produce flowers. Correlation coefficients for age of ortet (22 to 135 years) and flower production ranged from +0.28 to -0.25 (table 6), indicating that for this age group there was no relation. However, this data does not reflect the ages (3 to 6 years) of the ramets within orchards.

It is known that moisture stress can be an important factor in flowering and cone production (Sweet 1975). Correlation coefficients were computed to determine if there was a relation between total rainfall for a given month and the next year's flower production. During the summer of 1976, the seed orchard was subject to a prolonged drought. Weather records for 1976 show that the May through September rainfall was 46 percent below the average of the previous 4 years. We hoped that the drought would stimulate flower production in the seed orchards for 1977; the white spruce data show that flowering was dramatically increased in 1977 (table 3). The results for the seven orchards indicate that a correlation between June rainfall and flower production may exist (table 7). However, one must consider that this data only includes a single severe drought year and the results may be due to normal cyclic flower production.

CONCLUSIONS

Although the data presented here only covers a few years of production, it is encouraging to note the number of clones that have produced cones. Within a few years these orchards should produce sufficient seed to meet the needs of the National Forests in the Lake States.

The possible correlation between flowering and rainfall must be considered with other factors when selecting seed orchard sites, and will be useful in planning breeding work and cone collection operations. This relation could also become the basis for determining when to apply a flower induction treatment such as fertilizer. This may be a key to producing large amounts of flowers for breeding and production needs on a more regular basis.

In the future we will continue to observe the flowering-moisture relation. We may find that in order to be useful, correlations will have to be established for each individual orchard and perhaps even for individual clones.

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SEED PRODUCTION IN THE FIRST EIGHT YEARS AND FREQUENCY OF NATURAL SELFING IN A SIMULATED JACK PINE SEEDLING SEED ORCHARD

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ABSTRACT.-- Seed production and percent of natural selfing were determined in an 8 x 8-foot, 1200-tree plantation. Actual seed production was determined through age 6; production through age 8 was projected based on first-year cone counts at age 7. The percent of natural self-pollination, production of seedlings from natural selfing, and percent of selfs that were lethal were determined by marker seedlings. Ovulate strobili production began at 17 months of age; by age 4 a few trees produced small quantities of mature cones and seed. By age 8 years most trees produced an average of 39 mature cones per tree, 26,200 cones per acre, or 655,000 filled seed per acre. Total filled seed per acre produced through age 8 years was 1,159,000. The overall average of open-pollinated seedlings resulting from natural selfing was about 7 percent. The frequency of natural self-pollination, determined from carriers of selected seedling marker types, ranged up to 34 percent; on the average more than half of these were lethal. Removing trees showing high selfing percentages and careful culling of poorer seedlings grown from orchard seed before field planting should reduce the impact of natural selfing on wood yield in such plantations to a minimum.

Three important considerations for managing pine seed orchards are: how early do they produce seed, how much seed do they produce, and how much seed results from selfing?

Jack pine (Pinus banksiana Lamb.) begins to produce ovulate strobili in the third and fourth year when grown under standard nursery conditions (Righter 1939, Wright 1964, Rudolph 1966b), but as early as 17 months if started in the greenhouse under near-optimum conditions (Rudolph 1966b,

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Jeffers and Nienstaedt 1972). Once cone production begins it is fairly regular (Godman and Mattson 1976) and increases until crown competition becomes a factor (Roe 1963).

Jeffers (1976), using well-substantiated seed yields per cone (Schantz-Hansen 1941, Rudolf 1958, Roe 1963, Rudolph 1966b, 1967, Jeffers 1972), and actual female strobili per tree at age 5, predicted a yield of 267,000 full seed per hectare of jack pine seed orchard at age 6.

Most wind-pollinated seed produced on jack pine results from cross-fertilization but up to 25 percent naturally selfed seed has been reported in progenies of individual trees (Fowler 1965a, 1965b, Rudolph 1966a, Teich 1970, Sittmann and Tyson 1971). Hadders and Koski (1975) have reviewed the factors affecting the proportion of natural selfing in relation to production of seed in pine seed orchards. Selfing can result in reduced cone set, lower filled seed yield, poorer seed germination, lower survival of seedlings, depressed growth rate, and increased frequency of deviant types (Fowler 1965b, Rudolph 1966a, 1967, 1976), all undesirable features in seed orchard management.

In this paper I report the actual seed production in a simulated seedling seed orchard through age 6 from seed, the projected yields through age 8 based on first-year cone counts at age 7, and I estimate the frequency of natural selfing based on the proportion of various marker seedling types in open- and controlled self-pollinated progenies. I also recommend the means to reduce the effect of natural selfing on future wood yields.

MATERIAL AND METHODS

Trees for this study were grown from seed collected in August, 1960 from approximately 50 jack pine trees in an extensive stand near Rhinelander, Wisconsin. Variable quantities of seed per tree comprised the bulk lot. The primary objective of the study was to determine the effects of gamma irradiation of the seed at various exposure levels on the long-term survival and reproductive capacity. However, the design of the study, particularly of the field test, lends itself well for consideration as a simulated seed orchard. The radiation effects, which will be reported elsewhere, do not invalidate the seed production results to be presented here but do make the estimates slightly more conservative than could be expected without irradiation due to slightly lower production in the highly irradiated lots. The slight impact of irradiation noted on seed yield and self-ability will be discussed in the results section. Design details relating to radiation treatments will only be presented to put the total experiment into perspective.

In December, 1966, thirteen samples of 300 seeds each were fully imbibed in water. They were then gamma irradiated at one of thirteen exposures ranging to 19,200 R. The irradiated seedlots were divided into three replications of 100 seeds each and sown in sand in a greenhouse. At 1 month of age, 125 seedlings per exposure randomly chosen from the combined three replications were transplanted into 2½ in. x 2½ in. x 3 in. veneer plant bands, and randomly assigned to five replications of 25 seedlings each. The seedlings were grown in the greenhouse until May 1967 when they were transplanted to the Hugo Sauer Nursery near Rhinelander, Wisconsin. The same design as in the greenhouse was followed in the nursery but with a 7 in. x 7 in. spacing between plants. Incidence of flowering was scored on the nursery-grown seedlings in the spring, 1968 and percent of trees flowering and ovulate conelets per tree determined.

Approximately 1200 seedlings survived and were field planted near Lake Tomahawk, Wisconsin on June 10, 1969 at an 8 ft. x 8 ft. spacing inthe same randomized block design as was used in the nursery with 5 x 5 tree plots.

All open-pollinated cones produced in 1970, 1971, and 1972 (ages 4, 5, and 6 years) were collected separately from each tree each year. Seed was extracted by shaking the cones in a sieve with 1/4 in. x 1/4 in. openings following a brief dip in boiling water to open the cone scales. The seed was counted and X-rayed to determine percent filled. Percent of trees with mature cones and seed yields were determined.

In the spring, 1973, when the trees were in their seventh growing season, the total number of ovulate conelets per tree was scored on the center nine trees of each plot to facilitate estimation of cone production in 1974 or at age eight. Also in the spring, 1973, two trees that had relatively abundant male and female strobili production were selected in each plot for controlled self-pollinations. Whenever possible, trees in the same position within plots were selected to provide for a relatively uniform but representative selection of trees throughout the planting. Thus, a total of ten trees per each of the twelve radiation treatment levels (no trees survived in the 19,200 R treatment) or 120 trees were selected for the self-pollinations. Five isolation bags were placed on each tree and the female strobili in each of the 600 bags were self-pollinated on June 1 and 2, 1973. Mature cones from the self-pollinations were collected in late September, 1974, keeping those from each pollination bag separate. Five open-pollinated cones from each of the bagged trees were collected at the same time. Of the 120 trees self-pollinated, 106 produced a total of 1200 cones.

The selfed seed together with the sample of open-pollinated 1973 seed from five cones on the same trees was extracted by hand by removing the cone scales, counted, X-rayed to determine percent filled, and germinated in sand in the greenhouse. The seedlings were examined at frequent intervals for 3 months to search for characteristics with potential as genetic markers. Frequency of markers within individual tree progenies was expressed as a percent of total seedlings germinated.

A similar procedure for screening for marker seedlings was used to screen open-pollinated seed from all trees producing cones in 1972. Whenever possible, 200 filled seed from each of the 1178 trees producing cones was sown; however, fewer filled seeds were available from some trees. A "damping-off" fungus problem in one greenhouse bench during germination reduced the number of open-pollinated families that could be effectively screened to 848.

Percent of open-pollinated seedlings resulting from natural *self-fertilization* was determined for all families that were segregating for the various types of marker seedlings. It was assumed for simplicity, that the markers were recessive and that they segregated in a 3:1 ratio upon selfing; that is, the frequency of marker seedlings in the open-pollinated progenies was multiplied by four. The simplistic 3:1 ratio was assumed in this study because a genetic explanation for apparent deviations from this ratio observed in some families is not known.

Percent of natural *self-pollination* was calculated as the ratio:

$$\frac{\text{percent of marker seedlings in open-pollinated progenies}}{\text{percent of marker seedlings in controlled self-pollinated progenies}}$$

Application of this ratio assumes that self-pollen is as viable and active as cross-pollen and that one embryo occurs per ovule. It must be recognized that the percent of natural self-pollination determined in this manner may be over-estimated to an unknown degree due to possible mating between carriers of common markers.

The percent of *self-pollinations* that were lethal was determined from the relationship:

$$\frac{\begin{pmatrix}\text{percent of natural}\\ \text{self-pollination}\end{pmatrix} \text{ minus } \begin{pmatrix}\text{percent of open-pollinated seedlings}\\ \text{from natural self-fertilization}\end{pmatrix}}{\text{percent of natural self-pollination}}$$

RESULTS AND DISCUSSION

Cone and Seed Production

Ovulate strobili production began in the spring, 1968, in the nursery at approximately 17 months of age, on 28 percent of the trees (table 1). Of the total surviving trees, 21 percent had one, 6 percent had two, and less than 1 percent had three or four ovulate strobili per tree. Percent of trees flowering was significantly lower in some of the highest radiation levels. Thus, the overall average percent of trees flowering was below what might have occurred without irradiation (table 1). However, even with this decrease, the percent of trees producing ovulate strobili in this population is somewhat higher than that previously reported for 17-month-old seedlings (Rudolph 1966b, Jeffers and Nienstaedt 1972). Less than one percent of the trees produced male strobili at this age.

Table 1.--Ovulate strobili production in the nursery in 1968 on 17-month-old jack pine seedlings field planted into a simulated seed orchard the following year

Gamma exposure (R)	Total trees	Trees with: One ovulate strobilus	Two ovulate strobili	Three ovulate strobili	Four ovulate strobili	Total trees flowering:	
	Number	Percent	Percent	Percent	Percent	Number	Percent
0	112	28.6	1.8	2.7		37	33.0
150	117	20.5	12.0	1.7		40	34.2
300	102	23.5	8.8			33	32.4
600	120	25.8	2.5			36	30.0
1200	114	13.2	4.4			20	17.5
1800	96	22.9	4.2	1.0		27	28.1
2400	108	26.8	8.3	1.8		40	37.0
3600	100	15.0	4.0		1.0	20	20.0
4800	107	15.9	4.7			22	20.6
7200	90	23.3	4.4	1.1		26	28.9
9600	84	17.8	2.4	1.2		18	21.4
14400	49	16.3	8.2			12	24.5
Total or Mean	1199	20.8	5.5	0.8	0.1	331	27.6[1/]

[1/] Based on total trees flowering divided by total number of trees.

Practically all the cones aborted and no cones were collected in 1969. This was probably due to the transplanting to the field in June, 1969, and to the lack of pollen in the nursery in 1968. Probably for the same reasons, the percent of trees with mature cones at age four years in 1970, less than 16 percent, was only slightly over one-half as many as produced ovulate strobili in 1968 and less than two mature cones per flowering tree were produced (table 2). The ovulate strobili primordia for the 1970 cones were differentiated during the 1968 growing season in the nursery and possibly suffered high abortion from transplanting shock and lack of pollen in 1969. Similarly, only 10 seeds were produced per cone and only 23 percent of these were filled.

In 1971, at age 5, the proportion of trees producing cones increased to about one-half but the number of cones per cone-bearing tree was still only about two (table 2). However, the number of filled seeds per cone, seven, was three times that in 1970 but still far below normal even though more than two-thirds of the total seed was filled. This possibly resulted from a meager supply of pollen in 1970. The number of filled seeds produced per acre in 1971 increased to more than 12 times that in 1970.

A more abundant pollen supply on the orchard trees in 1971 was apparent because in 1972 at age 6, 22 seeds per cone were produced and three-fourths of them were filled (table 2). This, coupled with an increase in percent of trees producing cones to 93, and more than ten cones per tree, increased the yield of filled seeds per acre to more than 113,000. The total yield of filled seed per acre through age six years was more than 119,000.

Actual production per acre was higher than predicted by Jeffers (1976), who used ovulate strobili at age 5 for his prediction of production at age 6, even though there were only 681 trees per acre compared to 3000 in Jeffers' study. This was largely due to more cones per tree than predicted which was only partially offset by a lower yield of filled seed per cone, 16.5, rather than the 25 predicted by Jeffers (1976). As noted earlier, the relatively few filled seeds per cone at age 6 is due at least partially to insufficient pollen. Mass artificial pollination with pollen from selected trees would likely increase substantially the yield of filled seed in such young orchards. By age 7, there was enough pollen to adequately pollinate the ovulate cones that matured at age 8.

Yields of filled seed during the first 6 years in this study were also lowered by the choice of transplanting time in June, 1969. Transplantation to the field at this time possibly not only decreased the percent of trees with cones in 1970 but likely had an impact on the production in the next 2 years as well (table 2). If the seedlings had been transplanted in the late summer of 1968 when the primordia

Table 2.--Mature cone and seed production of jack pine trees 4, 5, and 6 years old from seed

Year	Total trees	Trees w/mature cones	Cones per tree		Seed per tree		Filled seed per tree		Seeds per cone	Filled seeds per cone	Total seed filled	Filled seeds per acre at 8 ft x 8 ft spacing
			All trees	Trees with cones	All trees	Trees with cones	All trees	Trees with cones				
	Number	Percent	- - - - -	- - - - -	- - - - -	- - - - -	Number	- - - - -	- - - - -	- - - - -	Percent	Number
1970	1187	15.6	0.3	1.7	2.8	17.7	0.6	4.1	10.4	2.4	23.3	439
1971	1183	47.0	1.1	2.4	11.6	24.7	8.0	17.0	10.2	7.0	68.6	5,429
1972	1178	93.0	10.1	10.9	221.2	237.8	166.7	179.2	21.9	16.5	75.4	113,513
TOTAL FILLED SEED PER ACRE PRODUCED IN THE FIRST 6 YEARS												119,381

for the 1969 female strobili were already differentiated--but in time to establish the seedlings in the field before winter dormancy--there would have been more 1969 female strobili and more differentiation of 1970 and 1971 strobili. In addition, pollen production could possibly have been greater, resulting in higher seed yields. However, further research is needed to verify the impact of transplanting time on early seed production.

The rapid subsequent rise in cone and seed production beyond age 6 years when the trees were better established in the field and pollen production was more abundant is evident from conelet counts made in 1973 at age 7. Almost 43 conelets per tree were found after natural pollination in the summer, 1973 after early abortion and/or abscission had occurred. Assuming an additional 10 percent cone loss between the first year and cone maturity (Rudolph 1976), about 39 cones per tree could be expected in 1974 at age 8. Using this information and the actual seed yields for the first 6 years the total yields of filled seeds through age 8 may be summarized as follows:

Total filled seed production per acre in 1970 (age 4), 1971 (age 5), and 1972 (age 6), (from table 2)----------	119,381
Ave. number of conelets per tree in summer, 1973 (age 7)---	42.75
Number of cones per tree maturing in 1974 (age 8) assuming additional 10 percent cone loss -------------	38.48
Number of cones per acre in 1974 (age 8) at 8 ft x 8 ft spacing (681 trees) -----------------------------	26,205
Number of filled seeds per tree in 1974 (age 8) assuming 25 filled seeds per cone --------------------	962
Number of filled seed per acre in 1974 (age 8) at 8 ft x 8 ft spacing (681 trees) -------------------	655,122
Number of filled seed per acre in 1973 (age 7) assuming mid-point between 1972 and 1974 -------------	384,317
Total filled seed production per acre through age 8 --	1,158,820

As pointed out earlier, the yields given above are somewhat lower than may ordinarily be expected with the same cultural methods due to the decreased yields at the higher radiation levels. Nevertheless, they indicate that substantial seed yields in jack pine seedling seed orchards can be expected 8 years from seed. Assuming that at least 90 percent of the filled seed is viable (personal observation), about

1 million seedlings per acre of seed orchard can be produced within 8 years. Higher yields could be expected with improved cultural methods and attention to avoiding transplanting shocks. Selection of trees for serotinous cones would permit storing earlier seed production on the trees until yields are high enough to make collections more economically feasible, perhaps beginning at age 8. Selections and thinning could then be applied to promote maximum cone and seed production on the remaining trees in subsequent years.

Frequency of Natural Selfing

Estimated percent of open-pollinated seedlings from natural self-fertilization averaged about 7 percent assuming the markers were a recessive trait segregating 3:1 upon selfing (table 3). This is based on the evaluation of 24 different markers within 567 open-pollinated families among 848 families screened. The range was from about 2 to 18 percent. Proportion of natural self-pollinations, not all of which would result in successful self-fertilization and selfed seedlings, cannot be estimated from open-pollinated progenies.

Note that the proposed markers from open-pollinated progenies were scored on seedlings 3 months or less old. Therefore, some of the supposed markers, particularly certain of the dwarf types such as the "typical" green dwarf (table 3), need to be verified when the seedlings are considerably older. This classification included all seedlings that showed greatly reduced growth at this young age; some of these slow-growers probably exhibited temporary non-genetic effects such as differences in seed size. Additional development will need to be observed and will undoubtedly result in a reduced number of carrier trees for dwarfism. Other characteristics now classified as markers may similarly prove to be temporary physiological effects with age.

Our previous experience has shown that two marker types, yellow-green cotyledons and light green cotyledons, are under rigid genetic control. And since both open- and controlled self-pollinated progenies were available with these markers, they were chosen for more detailed analysis of natural self-pollination frequency in open-pollination and lethality following self pollination (tables 4 and 5).

The average percentages of marker seedlings in open-pollinated progenies of trees carrying these two types of markers and used in the detailed analysis--3 and 5+ percent for the yellow-green and light green cotyledon types, respectively--were slightly higher than the average for all trees carrying these markers (compare table 3 with tables 4 and 5). An average of about 12 and 8 percent of the open-pollinated seedlings in progenies with the two marker types resulted from natural selfing (tables 4 and 5). The lower than expected estimates (assuming 3:1 segregation) of the percent of open-pollinated seedlings resulting from natural selfing in the light green cotyledon

Table 3.--Estimation of proportion of open-pollinated seedlings resulting from natural selfing from frequency of marker seedlings in 1972 open-pollinated progenies

Marker type	Carrier trees 1/	Marker seedlings within family	Open-pollinated seedlings from natural selfing 2/
	Number	Average percent	Percent
White cotyledons	4	2.0	8.0
Yellow-green cotyledons	28	2.6	10.4
Greenish-yellow cotyledons	9	1.2	4.8
Whitish-green cotyledons	6	4.2	16.8
Greenish-white cotyledons	4	1.7	6.8
Light green cotyledons	13	1.2	4.8
Yellow-green primary leaves	4	2.6	10.4
Bluish-green dwarf (typical)	75	1.3	5.2
Green dwarf (typical)	258	2.0	8.0
Bluish-green dwarf(extremely small)	5	1.1	4.4
Green dwarf (extremely small)	9	0.8	3.2
Short, fine primary leaves	1	1.2	4.8
Bluish-green dwarf w/early bud set	21	1.7	6.8
Thin, fine, short primary leaves	3	1.1	4.4
Bluish-green dwarf with thick, stiff primary leaves	7	1.3	5.2
Stem forked immediately	2	4.5	18.0
No apical meristem	8	1.8	7.2
Cotyledons emerge through seedcoat	72	2.2	8.8
Double embryo	18	1.5	6.0
Tightly fused cotyledons	2	3.0	12.0
Kinky stem	6	0.6	2.4
Reverse germination	9	1.8	7.2
Possible chimera (two shoot types)	2	0.7	2.8
Twisted and deformed primary leaves	1	0.6	2.4
Total	567 3/		
Mean		1.78	7.12

[1] Based on 848 parent trees screened.

[2] Assuming marker is a recessive trait segregating 3:1 upon selfing.

[3] 132 trees are carriers of more than one marker type.

marker type are at least partially due to three factors: (1) unexplainable large deviations from a 3:1 segregation ratio such as in tree 4-150-14 (table 5); (2) similar or higher percentages of marker seedlings in open- and self-pollinated progenies of some trees such as tree 4-7200-18 (table 5); and (3) possible differences in linkages of the marker in different trees with different lethal factors. Sorenson (1969, 1971) has found such distorted ratios due to embryonic lethals.

Estimates of the average proportion of natural self-pollination are over 34 percent as determined from the yellow-green cotyledon marker type (table 4) and over 20 percent as determined from the light green cotyledon type (table 5). However, in both cases, if a 3:1 segregation ratio for the markers is assumed, the average percent of lethals resulting from self-pollination is more than 50. This results in an average production of open-pollinated seedlings from successful self-fertilizations of from 8 to 12 percent and is sligthly higher than natural selfing in slash pine reported by Kraus (1975). The probability is that only one-fourth of these are homozygous recessive for any given deleterious gene. Thus, only 2 to 3 percent of the open-pollinated seedlings in a seed orchard as described here should be deleteriously affected by self-pollination and successful self-fertilization, even though the percentages of seedlings from selfing would be 4 times more. The percentages of natural selfing, as estimated in this study by the use of marker seedlings, may be slightly inflated in that marker seedlings resulting from possible crosses between carriers of common alleles are indistinguishable from selfed seedlings. The occurrence of trees with common marker alleles cannot be verified without controlled cross-breeding.

Such low percentages of seedlings showing the depressing effects of self-pollination may not be significant in production of genetically improved seedlings from seed orchards although occasional trees showing high selfing percentages should be removed from the orchard. Culling of this small proportion of poorer seedlings from the progenies before field planting should be easily possible. The small numbers of weak seedlings that remain would likely succumb soon under the more rigorous environmental conditions in present-day tree plantations and would have little influence on ultimate wood yield from such plantations.

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Table 4.--Estimation of proportion of seedlings resulting from natural self-fertilization, frequency of natural self-pollination, and percent of selfs that are lethal from frequency of seedlings with yellow-green cotyledons in open- and controlled self-pollinated progenies

Tree no.	Seedlings that are		Marker seedlings		Open-pollinated seedlings from natural selfing 1/	Natural self-pollination 1/	Selfs that are lethal 1/
	Open-pollinated	Self-pollinated	Open-pollinated	Self-pollinated			
	-------- Number	--------	-----------	-----------	Percent	-----------	-----------
1-600-3	229	112	2.6	6.2	10.4	41.9	75.2
2-1200-13	41	156	7.3	24.4	29.2	29.9	2.4
2-2400-13	125	38	2.4	2.6	9.6	92.3	89.6
2-3600-3	237	270	3.4	16.7	13.6	20.4	33.2
3-150-8	250	86	2.4	8.1	9.6	29.6	67.6
3-300-13	159	86	1.9	2.3	7.6	82.6	90.8
3-7200-8	166	76	3.6	15.8	14.4	22.8	36.8
3-7200-13	181	28	2.8	10.7	11.2	26.2	57.2
4-1200-3	197	109	1.0	4.6	4.0	21.7	81.6
4-4800-3	323	75	3.4	20.0	13.6	17.0	20.0
4-4800-18	145	238	2.8	7.1	11.2	39.4	71.6
4-9600-3	195	102	0.5	42.2	2.0	1.2	-- 2/
5-150-3	241	13	3.3	7.7	13.2	42.9	69.2
5-1200-18	172	268	3.5	14.6	14.0	24.0	41.6
5-1800-18	82	62	3.7	14.5	14.8	25.5	42.0
Total	2,743	1,719					
Mean			2.97	13.17	11.89	34.49	55.63

1/ Assuming marker is a recessive trait segregating 3:1 upon selfing.

2/ Cannot be determined on basis of 3:1 ratio.

Table 5.--Estimation of proportion of seedlings resulting from natural sel -fertilization, frequency of natural self-pollination, and percent of selfs that are lethal from frequency of seedlings with light green cotyledons in open- and controlled self-pollinated progenies

Tree no.	Seedlings that are		Marker seedlings		Open-pollinated seedlings from natural selfing [1]	Natural self-pollination[1]	Selfs that are lethal [1]
	Open-pollinated	Self-pollinated	Open-pollinated	Self-pollinated			
	-------- Number	-------	--------------------------	------------	Percent	-------------	-------------
1-1200-3	118	127	3.4	22.8	13.6	14.9	8.8
1-2400-3	213	87	1.9	9.2	7.6	20.7	63.2
3-150-18	239	158	0.8	5.1	3.2	15.7	79.6
3-300-13	159	86	2.5	8.1	10.0	30.9	67.6
4-150-14	214	192	1.9	55.4	7.6	3.4[2]	--[3]
4-7200-18	153	43	21.6	14.0	--[3]	--[3]	44.0
Total	1,096	693					
Mean			5.35	19.10	8.40	20.55	52.64

[1] Assuming marker is a recessive trait segregating 3:1 upon selfing.

[2] Not included in mean due to large deviation from 3:1 ratio.

[3] Cannot be determined on basis of 3:1 ratio.

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ROOTING OF CONIFER PROPAGULES

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ABSTRACT.--An outline of the general problems involved with the propagation of elite conifer clones by rooted cuttings is drawn from published reports. New approaches for resolving these problems can come from studies of clone production through tissue culture methods. Probable extension of tissue culture techniques will permit the establishment of clones from adult, proven trees and may also provide a tool for *in vitro* propagule evaluation of disease resistance.

Reforestation by vegetative propagation of select clones offers the possibility of rapid improvement of forest yield (Shelbourne and Thulin 1974, Kleinschmit 1974). Clonal reforestation will require a fresh consideration of forest management and the implied biological risks, but the potential for utilization of non-additive genetic variance in trees and the benefit where seed production is slow or inadequate are both strong motives for operational vegetative propagation. Two methods of vegetative propagation offer promise: (1) rooted cuttings or needle fascicles, and (2) rooted propagules produced through tissue culture. The potentials and problems for these two approaches are compared in this paper.

Rooted Cuttings

A comprehensive review of the various reforestation programs using clonal rooted cuttings is presented by Brix and van den Driessche (1977). Clone production by rooted needle fascicles of pine was reviewed by Girouard (1971). General review of rooting practice for horticulturally important species is treated in the book by Hartmann and Kester (1975). Clonal propagation of *Cryptomeria japonica* has been used for centuries in the forests in Japan and provides the only data concerning long-term benefits and problems. Major programs for propagation of Norway spruce with rooted cuttings for operational planting are underway in West Germany (Kleinschmit 1974) and Finland

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(Lepistö 1974). A major research effort with radiata pine is continuing in New Zealand and Australia (Sweet and Wells 1974, Shelbourne and Thulin 1974) but operational plantings are not yet a reality. Research programs for Douglas-fir (Ross 1975), loblolly pine (van Buijtenen et al. 1975) and western hemlock (Boyd 1976) are being conducted in the United States and for white spruce and black spruce in Canada (Rauter 1974).

The above programs are new in terms of forest tree harvest cycles and most of the information deals with rooting behavior and the early field performance of the propagules. Long-term field behavior will be forthcoming. Production of rooted cuttings is difficult or impossible for many species, but where problems can be overcome rapid production of select clones (1/2 million plants from one seedling in 5 years) seems possible. Fully operational cloned planting stock production could be implemented in 10 years given 4-year field evaluation. At that stage in program development the cost of propagules has been estimated at 2 to 3 times higher than for seedlings (Brix and van den Driessche 1977). Time and cost values must be weighed against tree improvement gains through cloning. Such gains can be great.

The problems associated with the production of rooted cuttings vary greatly with species and even individual tree within species. Generally, cuttings taken from young trees in the juvenile stage root more efficiently than cuttings from older trees in the adult stage, e.g., Douglas-fir (Ross 1975), radiata pine (Libby et al. 1972), and white spruce (Rauter 1974). For some species this is not so pronounced (western hemlock,Brix and Barker 1975) and for others even the juvenile stage shows low rooting efficiency (lodgepole pine, Longman et al. 1972) or poor root form (white pine, Thomas and Riker 1950).

The rooted cuttings may grow in the field at rates comparable to seedlings (Norway spruce, Lepistö 1974), or they may achieve these rates after a lag period (western hemlock, Brix and Barker 1975), or continue to grow more slowly (radiata pine, Sweet and Wells 1974). In addition to drastic differences in growth rate, rooted cuttings may assume an irregular growth form (plagiotropism) with age of parent tree or age and position of the shoot on the parent tree, e.g., Douglas-fir (Ross 1975, Copes 1976). On the other hand, rooted cuttings from adult trees may possess some desirable adult tree characteristics such as disease resistance (Thuja plicata, Søegaard 1956).

Overall, propagation by rooted cuttings varies greatly in the rooting efficiency and growth of cuttings from species to species and from tree to tree. Furthermore, the performance of cuttings may be affected profoundly by tree age, position of the cutting on the tree, tree vigor, and the season cuttings were taken. Many of these problems can be overcome in many species by refining methodology, but the solution of the general problems summarized in figure 1 remain.

The major dilemma with forest improvement through vegetative propagation by rooted cuttings is that cuttings propagate better from juvenile trees, but selection of elite mother trees must come after they have reached the adult stage; by then propagation by cuttings becomes a severe problem (fig 1). A practice of repeated shearing of juvenile trees, "hedging", has aided in retaining the juvenile character of cuttings over a longer period (Libby and Hood 1976). Repeated cycles using rooted cuttings as the source of new cuttings, "re-rooting", has also helped to maintain juvenility (Fielding 1969). These practices may be adaptable to a variety of species but, failing that, there remains the possibility of devising more reliable selection procedures for juvenile trees or of using methods that can generate cuttings of juvenile character from adult trees (fig. 1).

Tissue Culture Propagules

The recently emerging application of tissue culture techniques to conifers provides an alternative to rooted cuttings for clonal forest propagation. Present tissue culture techniques can provide rooted propagules of forest species from multiple adventitious buds formed on embryos or on embryo and seedling parts cultured *in vitro* (Mott *et al.* 1977 and references there cited). The present tissue culture capabilities are similar to those of the rooted cutting methods (fig. 1) in that rooted propagules may be produced in a short time from juvenile seedling material. Reliable and routine rooting of the shoots produced in culture, on the scale needed in operational planting, is difficult to achieve. Cost per tissue culture propagule is high and the propagules are just beginning to be field tested and are not ready for operational planting.

The only published data on propagule production from improved tree genotypes (Mott *et al.* 1977) shows that multiple adventitious shoots can be obtained from nearly all seedling progeny of select loblolly pine trees from piedmont or coastal plain sites. An average of 20 shoots per clone can be expected on the first cycle, but methods to root a high percentage of these shoots reliably and on a production scale are lacking. As much as 70 percent rooting of these shoots has been achieved in some experiments, but production of 3-10-rooted individuals per clone is more common. Work is continuing in the laboratory (Mehra-Palta *et al.* 1977) and elsewhere to improve the rooting efficiency.

The early growth and form in soil of such propagules compare favorably with those of seedlings, and clones of few individuals can be tested simultaneously on several sites, thus multiplying the information to be gained on genotype/environment interactions during the field tests. In this way the clones can aid efforts to develop reliable methods for selecting elite trees while they are still juveniles.

Figure 1.--Generalized outline of problem areas in the propagation of elite clones of conifers by means of rooted cuttings.

Possible improvements	Source of cuttings	Rooting	Propagule behavior in field
Increase selection efficiency for young trees	Juvenile Trees (poor clone selection at juvenile stage)	+ good efficiency - poor root form - variable with tree - season dependent	+ favorable comparison with seedling
Prolong juvenile phase (hedging; re-rooting)	↓		
Reversion from adult to juvenile phase	↓		
	↓		
Devise better means of rooting adult tree cuttings	Adult Trees (better clone selection at adult stage)	- poor efficiency: age/size of tree position on tree - poor root form - inconsistent rooting - season dependent	+ adult wood qualities + disease resistance - loss of juvenile growth - plagiotropism - abnormal growth

Obviously, the tissue culture methods are at a much earlier stage of development than rooted cuttings. But all indications are that the problems in rooting the adventitious buds from tissue culture will be resolved. Furthermore, there are similarities between the two technologies that might help to resolve some of the problems encountered with cuttings. Cuttings must be studied intact because they rely on photosynthesis and shoot growth to support root initiation. Consequently, subtle influence of the mother tree on the shoot growth behavior of cuttings is inherent in the rooting process. Tissue culture procedures offer a more tractable system for the study of the controlling factors in rooting. Carbon source, nutrients, and growth regulators are suplied in the culture medium and thus buds, shoots, stems, etc. can be excised and cultured separately to discover the influence of each on the rooting process. For example, growth regulators normally produced within the plant can be supplied exogenously in an effort to mimic the contribution made by the young shoot tip that has been removed. Finally, the more extensive information on growth behavior of rooted cuttings may point the way for tissue culture studies.

Some preliminary data from studies of basic rooting factors are summarized in table 1. Rooting efficiency in response to the growth regulators NAA (α-napthaleneacetic acid) and BAP (6-benzylaminopurine) is compared for seedlings lacking shoot and root -- "hypocotyl sections"; seedlings lacking roots -- "derooted seedlings"; the terminal growing bud of seedlings -- "excised seedling shoots", and for similar "adventitious buds" produced in culture. The rooting efficiency is affected by other factors including the age of the seedling and the culture environment, etc. These effects are reflected in the range of percentage rooting given for each growth regulator concentration in table 1.

Table 1.--Summary of *in vitro* rooting efficiency to be expected for different seedling parts and tissue culture buds in response to growth regulator stimuli

Growth regulator concentration (mg/l) supplied in agar medium		Percent rooting			
NAA	BAP	Excised hypocotyl sections	Derooted seedlings	Excised seedling shoots	Adventitious tissue culture buds
0	0	0-6	0-37	0	0
0.1	0	0-27	0-12	--	20-30
0.1	0.1	0-27	80-90	70-80	40-70
0	0.1	0	0-12	0	0

Experiments of this type suggest that different exogenous growth regulator supplies are needed depending on which parts have been excised. Further experiments should define corrective measures to be taken when certain parts of seedlings or shoots are absent or functioning improperly. This information should lead to more efficient methods for the rooting of cuttings from trees. For example, the poor rooting of cuttings taken from adult trees might be corrected by suitable treatments to improve the vigor of the shoot bud on such cuttings.

Buds of loblolly pine produced by tissue culture are adventitious and possess juvenile character. The adventitious buds may be obtained from seedling hypocotyl and stem sections and the adventitious buds themselves are capable of successive rounds of new adventitious bud formation. The juvenile character of adventitious buds so produced holds great promise for vegetative propagation of adult trees. Procedures are now being tested for adventitious bud production from cultured parts of older trees. These buds develop on parts cultured after removal from influence of the adult mother tree, so they can be expected to revert to juvenile character. Once established, the adventitious buds could be used in successive rounds of propagule generations in the short time and small space characteristic of tissue culture propagation of herbaceous plants (Murashige 1974). This would, of course, permit vegetative propagation of elite trees selected in the adult stage (fig.1).

Adventitious buds can be obtained from continuously subcultured, disorganized callus cultures of aspen but there is evidence that clones produced in this way may not be uniform (Lester and Burbee 1977) and this might argue for bud production from excised tree parts rather than from subcultured callus.

Propagule Evaluation *in vitro*

It seems certain that the methods for rapid vegetative propagation of conifers on a production scale will soon be at hand. The capacity of rapid propagation brings with it the need for early and efficient testing for such things as disease and pest resistance. An elite adult tree may have merely escaped certain diseases in its present site; the propagules may present a substantial hazard for other sites. Early selection for resistance in the laboratory on cultured tissues would permit tests for disease resistance to keep pace with potential propagule production. Tissue culture may also provide a more tractable system for study of mechanisms of disease resistance, similar to the approach outlined earlier for rooting.

We have succeeded in rearing southern pine beetle from eggs on a loblolly pine callus substrate (Mott and Thomas 1977). This system can now be used to study pest/host interactions and host resistance. Fusiform rust resistance of young loblolly and slash pine seedlings and excised seedling parts can be identified in culture and the rust may also be cultured axenically (Amerson and Mott, in press). This opens the way for pathogen/host interactions and disease resistance mechanisms to be studied on this and other important diseases under controlled *in vitro* conditions.

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MASS PRODUCTION ALTERNATIVES FOR FAST-GROWING SPRUCE HYBRIDS

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ABSTRACT.--A reciptrocal crossing program of Picea glauca and P. omorika, and P. mariana and P. omorika with adequate intraspecific control crosses was carried out. Yields of full seed/cone ranged from 0 to 2.6 for the P. glauca-P. omorika combination. These low seed sets and a 9-day difference in female receptivity rule out producing this hybrid via seed. The full seed/cone yields of the P. mariana-P. omorika combinations averaged approximately half the yield of the intraspecific crosses. However, receptivity of the two species is well synchronized and in spite of reduced yields, mass production via seed is a practical option. A seed orchard design is outlined and a 4-acre grafted orchard may produce at least 75,000 plantable seedlings on 6- to 8-year-old grafts. Results of a rooting trial of selected hybrid seedlings are described. A practical mass production program for the P. glauca-P. omorika combination based on rooted cuttings is described. The program would be based on juvenile selection among 4-year-old seedlings, cloning, and the simultaneous establishment of clonal trials and hedges. The hedges would be a source of cuttings for future mass production--a hedge 400 feet long by 5 feet high would produce a minimum of 20,000 cuttings annually.

In 1959 a single cross between native Picea mariana and P. omorika was produced at Rhinelander, Wisconsin. Seed set was high and height growth of the hybrid was superior to the native species.

A P. omorika x P. glauca cross was first produced in 1964. In the greenhouse, mean early height growth of the hybrid exceeded the growth of P. glauca by 45 percent, and in 1975 in a field test exceeded the open-pollinated progeny of the P. glauca by 14 percent. The 1964 control cross P. omorika x P. omorika produced 9.8 full seeds per cone; in comparison the interspecific cross yielded 7.4

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seeds/cone. Both values are low, because up to 60 to 80 filled seeds per cone have resulted from other *P. omorika* x *P. omorika* crosses. Comparison among the 1964 crosses, however, suggested that the two species were cross compatible and that *P. omorika* x *P. glauca* crosses generally would result in high seed yields.

In 1971 both crosses were repeated on a larger scale with adequate controls to verify the superior growth of the hybrids and to determine the potential for mass production by seed. This trial clearly showed that *P. omorika* x *P. mariana* can be readily produced by seed on a large scale but that other means of reproduction must be found for the *P. omorika* x *P. glauca* hybrid. In 1975 a study was begun to test the possibility of vegetatively propagating *P. omorika* x *P. glauca* by means of cuttings.

It is the purpose of this paper to compare the sexual mass production with the vegetative mass propagation of these two promising spruce hybrids. The emphasis will be on propagation potential; performance of the hybrids will not be discussed.

SEXUAL MASS PRODUCTION OF HYBRIDS

Methods

Three individuals of each of *P. glauca*, *P. omorika*, and *P. mariana* were selected for vigor and the combinations *P. glauca*-*P. omorika* and *P. mariana*-*P. omorika* were tested. Intraspecific crosses were used as controls.

The selected *P. glauca* parents have been included in many tests to date and their progenies have consistently been top performers. The 1971 pollinations were made on 1959 grafts growing near Lake Tomahawk, Wisconsin.

P. mariana and *P. omorika* selections were made in a 1936 planting of spruce species growing on an upland site in Forest County, Wisconsin. Vigor of the trees was the only selection criterion.

The crossing scheme, including reciprocals, should have yielded the following number of crosses:

Combination	No. of crosses
glauca - *omorika*	18
mariana - *omorika*	18
glauca - intraspecific	6
mariana - intraspecific	6
omorika - intraspecific	6
	54

Due to lack of female conelets, particularly on *P. omorika*, only 44 of the crosses were attempted and of those 42 actually produced seed. In addition the three *P. omorika* trees were used as male parents in six crosses with two additional *P. omorika* genotypes and the three *P. glauca* genotypes were crossed with a random mixture of *P. glauca* pollen.

For *P. glauca* and *P. mariana*, fresh 1971 pollen collections extracted and cleaned at the laboratory were used. Pollen collected in 1970 and stored under various conditions were used for *P. omorika* crosses on *P. glauca* and on the two *P. omorika* genotypes. However, because no meaningful storage effects could be identified on either inter- or intraspecific crosses, the seed yield data were combined. A mixture of pollen from the various storage conditions was used to pollinate the three *P. omorika* and the three *P. mariana* trees in the Forest County, Wisconsin, test plantation.

Bagging of *P. glauca* was on May 10, 1971, and the later-developing species were bagged when the female strobili could be recognized. The following schedule shows the time of pollinations, debagging, and cone harvest:

♀ Species	Pollination	Debagging	Cone Harvest
		1971 Date	
P. glauca	5/21	6/4 - 6/8	9/1
P. omorika	5/30	6/11	9/21
P. mariana	5/30	6/11	9/9 - 9/21

For each pollination bag harvested, cones were counted and each individual cone extracted by hand to assure that *all* seeds were extracted. After dewinging and cleaning, the total sample was X-rayed and the number of full seeds counted on the X-radiographs. Last, the total number of seeds was sampled from eight bags on each of the three *P. glauca* and two to three bags in the case of *P. mariana* and *P. omorika*. From these counts the average total number of seed and full seed per cone were determined.

Unpollinated control bags were placed on all trees and only one bag on *P. omorika* yielded seed.

Results and Discussion

Seed yields in intraspecific crosses

The three *P. glauca* crosses (two diallels and one with mixed pollen) averaged 34, 43, and 47 full seeds per cone (for 1885, 1887, and 1889, respectively). These values compare favorably with previously published values for the same clones (Nienstaedt and Jeffers 1970, King *et al*. 1970). For individual crosses, yield of full seed ranged from 22 to as high as 73 (table 1). The latter value is higher than any previously published (Nienstaedt 1972). The results of the individual crosses suggest that clone 1889 is more productive than either 1885 or 1887; this substantiates previously published results (Nienstaedt and Jeffers 1970, King *et al*. 1970).

In the three *P. mariana* trees the two diallel crosses per tree averaged 27, 38, and 14 full seeds per cone for trees 5343, 5344, and 5340 respectively, and ranged from 11 to 38 full seeds per cone for individual crosses (table 1). These results are good because *P. mariana* cones usually average 43 full seeds per cone.

Table 1.--Yield of full seed from diallel crosses of three selected trees

Picea glauca

Female parents	Male parents			
	1885	1887	1889	Random mix
1885	0[2]	32 127	37 83	23 88
1887	22[1] 29	0	54 54	39 18
1889	58 38	42 79	0	73 37

Picea mariana

Female parents	Male parents		
	5343	5344	5340
5343	0	27 78	27 90
5344	38 75	0	38 99
5340	17 36	11 36	0

Picea omorika

Female parents	Male parents		
	5342	5347	5341
5342	0	46 39	74 22
5347	0	0	0
5341	68 4	78 2	0

[1] 22 = No. of full seed per cone.
29 = No. of cones harvested.

[2] 0 = Cross not performed.

The sample of 20 cones from the three *P. omorika* trees averaged a total of 87 seed per cone. The diallel crosses were only completed on 2 of the 3 trees and on the average yielded 56 and 71 full seed per cone on trees 5342 and 5341, respectively. The overall average was 57 full seed per cone. For individual crosses, yields ranged from 46 to 78 full seed per cone (table 1). This also shows that pollen quality and timing of pollination was good.

Seed yields in interspecific crosses

Contrary to expectation, the crosses between *P. glauca* and *P. omorika* yielded little or no seed regardless of the direction of the cross (tables 2 and 3).

Table 2.--Yield of full seed from diallel interspecific spruce crosses

Picea glauca and *Picea omorika*

Female parents of *Picea glauca*	Male parents *Picea omorika* 5342	5347	5341	Female parents of *Picea omorika*	Male parents *Picea glauca* 1885	1887	1889
1885	0.06[1] *839*	0.04 *615*	0.11 *666*	5342	0.68 *57*	2.61 *31*	0.43 *46*
1887	.14 *503*	.01 *272*	.15 *154*	5347	.00 *7*	0[2]	0
1889	.04 *479*	.04 *292*	.05 *756*	5341	1.67 *3*	2.33 *3*	.00 *1*

Picea mariana and *Picea omorika*

Female parents of *Picea mariana*	Male parents *Picea omorika* 5342	5347	5341	Female parents of *Picea omorika*	Male parents *Picea mariana* 5343	5344	5340
5343	11 *99*	13 *70*	22 *140*	5342	49 *13*	44 *49*	74 *4*
5344	14 *42*	18 *70*	21 *72*	5347	0	0	0
5340	5 *44*	5 *53*	7 *26*	5341	0	0	0

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[1] .11 = No. of full seed per cone.
666 = No. of cones harvested.

[2] 0 = Cross not performed.

Table 3.--Average yields of full seed/cone from diallel intra- and interspecific spruce crosses

Cross combination	Cones	Full seed	Ave. full seed/cone	Ave. seed/cone[1]	Full Seed
	- - - - - - - - -	- -Number- -	- - - - - - -		Percent
P.omorika x P.omorika	256	7,695	30.1	86.67	35
P.omorika x P.glauca	66	3,090	46.8	90.55[3]	52
P.mariana x P.mariana	414	12,130	29.3	43.03[2]	68
P.mariana x P.omorika	612	8,907	14.6	43.03[2]	34
P.omorika x P.glauca	148	152	1.0	86.67	1
P.glauca x P.glauca	553	21,564	39.0	71.33	55
P.glauca x P.omorika	4,576	312	.07	71.33	.1

[1] Unless footnoted, the derivation of these values is explained in the text.

[2] Based on counts of all bags with P. mariana x P. mariana crosses -- a total of 414 cones.

[3] Based on counts of 11 cones from tree 5342 -- the only tree in the cross.

Crosses between P. mariana and P. omorika, on the other hand, were successful. The average yield of full seed per cone when P. mariana was the female parent was 14.6 seed, about half the amount of seed obtained in the intraspecific P. mariana crosses (table 3). Mean full seed per cone yields of individual mother trees were 16, 18, and 5 seeds per cone for trees 5343, 5344, and 5340 as compared to the 27, 38, and 14 full seeds obtained from the intraspecific crosses. Individual crosses yielded from 5 to 22 full seeds per cone (table 2). Lowest yields were on tree 5340, but the cones on this tree contain only 19 seeds per cone as compared to 43 for 5343 and 53 for 5344. Nevertheless, 5340 appears to be the least cross compatible of the three trees--full seed yield was 27 percent of total seed yield as compared to 37 and 34 percent for the other trees. Unfortunately, it was only possible to perform the P. mariana crosses on one of the P. omorika trees--5342. This tree is characterized by a total yield of 91 seeds per cone and yielded an average of 56 full seeds per cone in intraspecific crosses--62 percent of total seed set. The seed yield for P. mariana crosses was almost as good (tables 2 and 3) averaged 47 seeds per cone (52 percent of total seed set).

Discussion

The above yields of seed clearly show that sexual mass production of hybrids between *P. glauca* and *P. omorika* is impractical. The 9-day difference in the phenology of the two species would necessitate an artificial pollination technique. But even if a practical mass pollination technique could be developed, the low seed yield would present an insurmountable obstacle.

It is, on the other hand, feasible to sexually mass produce hybrids between *P. omorika* and *P. mariana*. Phenologically, the species are well synchronized and even though the seed sets are reduced, they are still substantial.

The three crosses on the *P. omorika* parent (5342) suggest that it would be best to use *P. omorika* as the female. Other evidence supports this conclusion. In 1960 seed was collected from nine *P. omorika* trees growing near Eagle River, Wisconsin. Plots of *P. mariana* are located close by in the same test.[2] The progenies were planted in 1965 near Lake Tomahawk. In 1975, 129 of the original 180 trees had survived and of the survivors, 86 were identified as hybrids between *P. omorika* and *P. mariana*. Allowing for differential survival, we estimate that between 50 and 60 percent of the original trees were of hybrid origin. Hybrids were found in every progeny and must have represented from about 30 to as much as 90 percent of the trees in individual families. Thus, *P. omorika* 5342 isn't an isolated case of high cross compatibility between the two species. All the nine trees in the progeny test must have been phenologically well synchronized with the adjacent *P. mariana* and generally are cross compatible.

VEGETATIVE MASS PRODUCTION OF HYBRIDS

Vegetative propagation has been suggested as an alternative to sexual propagation of cross incompatible species combinations (Roulund 1971)and several schemes have been suggested for mass propagation of juvenile selections of various *Picea* species (Rauter 1974, Kleinschmit 1974, Kleinschmit *et al*. 1973, and Roulund 1976).

King *et al*. (1965) have shown that juvenile selections in 2-2 *P. glauca* retained superiority 7 years after field planting; more recent measurements at 22 years have shown that the selected seedlings are still 30 percent taller than the control trees.

In 1974 a study of selected juvenile *P. glauca* mass propagation by cuttings was begun and in 1975 it was extended to include the hybrid progenies described in the previous section.

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[2] The *P. omorika* and *P. mariana* parents of the crosses were from the same tests.

Source of Material

The seed was cleaned by blowing and for some samples by submerging in 95 percent ethanol to remove empty seed. Seeds were sown in perlite in glass-covered stainless steel trays on Jan. 29 and 30, 1973. The trays were kept in the greenhouse at 20-25°C and received 18-20 hours of light each day. The major period of transplanting was February to March, but lower than expected germination and unexplained seedling mortality necessitated resowing and replacement of some progenies in early May. Seedlings were transplanted into Ontario 5/8 inch tubes in a 1:1:1 sand-soil-peat mixture. In August the seedlings were transplanted to the nursery. Shade was provided initially.

The tallest 104 seedlings were selected during the summer of 1976. They represented all inter- as well as intraspecific combinations except _P. omorika_ x _P. omorika_. In addition, six _P. glauca_ and seven _P. mariana_ seedlings of average heights were selected as controls. The mean height superiority of the selected seedlings is expressed by the following values:

Parent combination	Mean ht. superiority over mean ht. of control
	percent
P. glauca x _P. glauca_	103
P. glauca x _P. omorika_	78
P. mariana x _P. mariana_	39
P. mariana x _P. omorika_	52

Cuttings were taken from the plants with pruning shears. They were 7-1/2-to 9-cm-long first and second order branch terminals. The top whorl was too coarse to be used. Cuttings were immediately put in plastic bags on ice in a cooler and within 24 hours were placed in the rooting bench.

Rooting environment

Rooting was on an open greenhouse bench provided with an automatic mist system, bottom heat, and an incandescent floodlight system to extend the photoperiod.

Air-temperature was set at 21°C (70°F) but substantially exceeded this on sunny days.

Media temperature was set at 26 to 29°C (79 to 84°F) but reached 32° (90°F) on sunny days, which damaged the cuttings.

Mist was applied for 15 seconds every 15 minutes during the day and 15 seconds every 30 minutes during the night.

The aim was to keep the cuttings constantly wet without excessive run-off but on sunny days the tops of the cuttings were dry on part of the bench. Also, because the water was hard, it covered cuttings with salts.

Media was gravel - peat - medium grade perlite, 1:1:1. Gravel was obtained by sifting pit run sand through 1/8-inch hardware cloth. pH was 4.0 initially and gradually increased to 6.0, a more favorable level.

Light regime was 19 hours photoperiod.

Fertilizer was applied weekly after rooting by drenching with Peter's Fertilizer (20-20-20) at a 1:128 ratio.

Cooling-off period consisted of reducing mist to 15 seconds every 30 minutes during the day and 15 seconds every 45 minutes during the night.

Newly transplanted cuttings were also kept under mist for a short period of time.

Experimental design

Containers were "Fives" rootrainers by Spencer-LeMaire[3]. One book of five cavities constituted a plot. Plots were arranged in five randomized complete blocks on a greenhouse bench.

Rooting schedule

September 27 and 28, 1976	Collection of cuttings
September 28 and 29, 1976	Sticking of cuttings
December 6, 1976	Cooling off period begun
December 23, 1976	Fertilizer treatment begun
January 7 to 26, 1977	Root evaluation and transplanting to 4 inch clay pots.

Results and Discussion

Rooting of clones of intraspecific crosses and control seedlings

In total, we rooted 16 clones of *P. glauca* (10 from selected seedlings and 6 from controls) and 29 clones of *P. mariana* (22 selected for vigor and 7 controls).

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[3] Mention of trade names does not constitute endorsement of the products by the USDA Forest Service.

The mean rooting percent for selected P. glauca and P. mariana clones was close to 50 percent. P. glauca controls did not root as well (42 percent) as the P. mariana controls (63 percent) (table 4).

Table 4.--Cuttings rooted from selected Picea glauca and P. mariana clones
(In percent)

Picea glauca

Female parent	Male parent 1885	1887	1889
1885		40.0 3[1]	48.0 1
1887			54.0 2
1889	54.0 4		

All 10 clones $\bar{x}$ = 49 percent

Control	
4885[2]	42.0 6

Picea mariana

Female parent	Male parent 5340	5343	5344
5340			58.7 3
5343	48.0 4		
5344	49.0 8		

All 15 clones $\bar{x}$ = 51 percent

Select 7169[3]	49.1 7
Control 7169[2]	62.9 7

[1] *Number of clones included in the mean values.*

[2] Open pollinated unselected control clones.

[3] Open pollinated seedlings selected for vigor and cloned.

Variation among individual clones was large and statistically significant. P. glauca rooting percentages ranged from 20 to 88 for selected clones and from 8 to 76 for control clones. Comparable values for P. mariana were 16 to 80 and 44 to 76 percent for selected and control clones, respectively. Rooting equaled or exceeded 60 percent in 30 percent of the selected P. glauca and 36 percent of the selected P. mariana clones.

Rooting of clones of interspecific crosses

Mean rooting of four P. glauca x P. omorika and five clones of reciptrocal crosses was 67 and 56 percent, respectively. For individual clones in the two groups, rooting percentages range from 36 to 92 and from 36 to 68 percent, respectively (table 5). The data suggest that the hybrids are better rooters than _P. glauca_ crosses and controls, but the differences are not statistically significant. The number of roots per cutting showed a similar and significant trend.

Table 5.--Cuttings rooted from selected clones of hybrids of _Picea omorika_, _P. glauca_, and _P. mariana_

(In percent)

P. glauca and _P. omorika_

Female parent of _Picea glauca_	Male parent of _Picea omorika_			Female parent of _Picea omorika_	Male parent of _Picea glauca_		
	5342	5347	5341		1885	1887	1889
1885				5342		52 *2*	
1887		92 1/ *1*	70 *2*	5347			
1889			36 *1*	5341		59 *3*	

All 4 clones x̄ = 67 All 5 clones x̄ = 56

P. mariana and _P. omorika_

Female parent of _Picea mariana_	Male parent of _Picea omorika_			Female parent of _Picea omorika_	Male parent of _Picea mariana_		
	5342	5347	5341		5343	5344	5340
5343	62 1/ *5*	76 *1*	74 *2*	5342	65 *3*	55 *11*	65 *28*
5344	48 *2*	47 *3*	48 *6*	5347			
5340	50 *2*			5341			

All 21 clones x̄ = 55 All 42 clones x̄ = 63

1/ *Number of clones included in the mean values.*

Overall, the rooting of the clones of the P. mariana and P. omorika combinations were comparable. Forty-two P. omorika x P. mariana clones had a mean rooting value of 63 percent and 21 clones of the reciprocal combination had a mean rooting value of 55 percent. The ranges in rooting percentages within these two groups were large; from 36 to 96 percent for the crosses in which P. omorika was the female parent and from 12 to 84 percent when the mother was P. mariana. The data in table 5 suggest that the ability to root is under strong genetic control; however, although the differences in rooting percent of individual clones were highly significant, the analysis of variance could not demonstrate significant parent tree effects. The number of roots per cutting was also determined and for this characteristic parent tree as well as clonal effects were significant.

Discussion

Because the environmental control was inadequate, rooting was less than anticipated for juvenile material. Two blocks on one end of the greenhouse bench had particularly poor rooting success. Therefore, the rooting in the three other blocks may be a better indication of the rooting potential of the clones. As an example, for all 5 blocks the rooting in 52 (47 percent) of the clones equaled or exceeded 60 percent. In the 3 better blocks, 82 (75 percent) of the clones attained this level of rooting. It is likely that even better rooting can be achieved if optimum conditions could be attained for an entire test (Kleinschmit 1974).

Mass production is only practical if large numbers of propagules can be produced for an extended period of time. But time connotes aging and rooting ability declines as stands mature. Hedging may be one answer to the problem (Libby 1974).

CONCLUSION

P. omorika x P. mariana seed production will require grafted seed orchards. Two orchard designs are possible:

(1) A simple two clone design -- in such an orchard, seed would be harvested on both the P. omorika and the P. mariana clone and, except for a small portion of selfed seed, would all be expected to be of hybrid origin.

(2) Orchards of one P. omorika clone and several P. mariana clones--hybrid seed would be harvested only on P. omorika. Whether or not the seed on P. mariana would be harvested would depend on the intraspecific general combining ability of the P. mariana clones. Good combiners could yield improved P. mariana seed. A small admixture of hybrid seed could probably be expected, but should not deter from the quality of the material.

The performance of the progenies involved in the studies I have discussed indicate the desirability of control-pollinated progeny testing before or concurrent with seed orchard establishment. Only three parents of either species were tested, but heights of progenies clearly showed that one P. mariana was a superior general combiner. This consideration may favor the orchard with many P. mariana clones. Inferior clones could be rogued on the basis of progeny test results.

Early productivity of seed orchards can perhaps be roughly estimated. P. omorika is not a prolific cone producer, but it might produce 10 cones per ramet at 6- to 8-year from grafting. With this assumption, a 4-acre orchard with 1,250 grafts (10 x 12 foot spacing)--250 P. omorika and 1,000 P. mariana (20 clones of 50 ramets each)--would produce 117,000 full seed (46.8/cone, table 3) which may yield approximately 75,000 plantable seedlings.

P. glauca x P. omorika or reciprocal hybrids would have to be vegetatively mass produced. A practical program may be as follows:

(1) Use 20 to 30 select P. glauca and 5 to 10 select P. omorika to produce 150 to 200 crosses between the two species. The majority of crosses should be on P. glauca and each cross should involve a minimum of 500 conelets. A program of this magnitude would probably produce from 3,000 to 6,000 hybrid seed.

(2) Fall sow in greenhouse and spring plant in the nursery at 18 x 18 inch spacing. If enough seedlings are available, an adequate statistical design should be used.

(3) At the end of the fourth season in the nursery, select the best 6 seedlings in the best 20 families.

These 120 seedlings will form the basis for the following clonal testing and mass propagation scheme:

First year. In the fall, stick 40 cuttings per clone. Discard all clones with less than 25 rooted cuttings.

Second year. In the fall, plant

(1) short-term clonal nursery test using single tree plots with 15 replications.

(2) at least 10 ramets for each clone selected on the basis of rooting, in double-row hedges with 1 foot between plants and 1 foot between rows (hedges would be 8 feet from center to center).

Third year. In the fall, stick 75 cuttings per clone--3 from each ramet in hedge as well as test.

The program in subsequent years may either seek the earliest possible production of stock for field planting or may aim at rapid build-up of the hedges. The clones will be evaluated at 5 years after the establishment of the test (7 years from the beginning of the program).

During the same period, it should be possible to establish 400 to 500 feet of double row hedges of each clone. If five cuttings could be produced per square foot of hedge, a 400-foot hedge 5 feet high would produce 20,000 cuttings, which would be 12,000 to 16,000 plants for field planting annually.

The productivity of the total program would, or course, depend on the final number of clones included in the hedge collection. If 30 clones of the original 120 were retained, we could expect from 360,000 to 480,000 plants from approximately 2-1/4 acres of hedges.

The program as outlined will be time-consuming and probably involve a minimum of selections. It could readily be increased without increase in the rooting facility if new clones were added each year by winter propagation. Profitability will depend on the gains in growth and frost resistance.

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IMPROVED TREES: ECONOMIC PROMISES AND PITFALLS

George F. Dutrow[1]

ABSTRACT.--Surging demands for wood fiber that must be produced on a decreasing acreage of forest land suggest soaring prices, a shrinking market for wood products, or both. Either of these consequences can be forestalled or prevented by implementing existing technologies, one of which is cultivation of genetically improved trees. Multiple and sizable gains from improved trees are likely. Gains are not without risks, however, as possible losses may occur through failure to accumulate capital necessary to establish plantations of improved trees on good sites.

Reasons for widespread reliance on improved trees are plentiful and pressing. Almost daily, trade announcements and public media forewarn of escalating demands for wood fiber from a diminishing land base. Like a mathematical equation, the oft reported and most assured result is a shortfall in timber supplies, signaled initially by soaring prices, and quickly followed by deteriorating markets as competing materials replace wood. Whether these calamitous outcomes are forthcoming is a matter of speculation, but the ability of improved trees to ameliorate such dire consequences is unquestioned. As a means to increase and improve the nation's wood supply, the genetically improved tree has no peers.

Yet, use of genetically improved trees is not without risk. In this paper, I emphasize probable gains and economic promise, but also describe hazards. I also review a method for analyzing the economics of tree improvement recently advocated by Clark Row and me.

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MORE WOOD FROM FEWER ACRES

A program to provide improved planting stock calls for substantial investments of money, land, and labor. All these productive resources could be profitably used elsewhere; they remain in timber production only as long as rewards are high enough to keep them there. Strong and stable demands for wood for the foreseeable future underlie decisions to commit resources to timber production. Thus, it behooves us to briefly examine the probable strength and durability of the demand for wood.

Most experts anticipate an upward climb in the demand for wood fiber (Armitage 1976, Zobel 1977b). Consumption of wood by the entire world is expected to rise from 95 billion cubic feet in 1975 to 140 billion cubic feet in 1990, an increase of approximately 50 percent in only 15 years (Armitage 1976). Worldwide pulpwood consumption is projected to rise even faster, doubling by 1985. Reports published by the USDA Forest Service project steep increases in consumption for industrialized nations, especially the United States, Japan, and countries in western Europe (Phelps 1975).

A significant hike in the supply of timber could prevent price increases, but even optimists are projecting, at best, a modest increase in available wood on the world market. Thus, the present trend of rising relative prices for wood and wood products will likely extend indefinitely into the future. And, investments in tree-improvement programs will probably not be buffeted by waves of dwindling demand.

Major additions of land devoted to timber production cannot be expected. In fact, historical evidence and a parade of prognosticators assert the opposite; i.e., land devoted to commercial production of wood fiber has declined and will continue to do so. Not only is forest acreage declining, but the more productive lands often are among the earliest casualities. Many productive sites are diverted to agricultural crops as landowners seek higher profits. Rich soils in bottomlands face a similar fate or inundation. And, sites both rich and poor face limitations on commercial timber production as environmental restrictions are imposed.

The Mississippi Delta offers an example (Sternitzke and Nelson 1970). Since the earliest surveys in the 1930's, almost 40 percent of the 12 million acres of commercial forest land has been lost to other uses. Even land held by forest industries has declined because of the lure of higher profits in other land uses. Loss of quality land is underscored by the growing percentage of forest acres of species that inhabit only poorly drained clay flats. Forestry's losses were gains for soybeans, improved pastures, and cotton, in that order.

Without further belaboring the point, it appears certain that demand for wood fiber will remain strong and that timber supplies will come from a smaller land base. Such circumstances suggest that prudent investments to augment timber supplies will be profitable. One such investment of proven value is in tree improvement. Economic analyses paint an encouraging benefit--cost picture for tree-improvement programs as a means of accelerating per acre production of wood.

BENEFITS OF IMPROVED TREES

In considering the host of benefits that reputedly accrue to the new subscriber to improved trees, a critical oversight frequently occurs. Tree improvement is pictured as independent of other recommended management practices. No assumption about improved trees is more likely to reap financial havoc. Yield increases promised for genetically-improved planting stock occur only when properly combined with site selection, site preparation, fertilization, and silvicultural maintenance. Gains from improved trees, as with most intensive forest practices, demand close adherence to a series of recommended treatments. Attempts to reduce costs or cut corners in silvicultural prescriptions will likely erase gains. Benefits are listed here in the context of fully integrated forest management.

Much attention and effort in the South have been directed to pines, but hardwood tree-improvement programs are also well underway, and hardwoods promise to respond well to improvement efforts. Demand for pine stumpage, markets for pine products, relative ease with which pines can be genetically improved, and overall economy, however, have dictated some neglect of hardwoods and concentration on softwoods. Thus, most gains and analyses mentioned in this paper pertain to softwoods.

Overall objectives of tree improvement programs read like familiar sign posts: faster growth rates, increased resistance to forest pests, better tree form and wood quality, and heightened adaptability. If our storeroom of economic data were replete with necessary and accurate information, and if our markets fit the requirements of perfect competition, then our economic analyses could clearly assess costs and benefits of each stated objective. In the absence of both data and free markets, we can only roughly estimate probable gain. Nevertheless, one conclusion surfaces over and over: improved trees promise substantial financial reward at minimal cost, especially for industrial landowners. This beneficial ratio stems largely from gains in specific tree characteristics which individually and collectively enhance the value of the wood for processing. Furthermore, small per-acre gains in desirable characteristics become significantly more important when measured over large tracts of managed forest lands.

Volume gain is a primary goal for most tree-improvement programs. Early advocates of genetic improvement predicted volume gains in excess of 50 percent, but current workers expect volume increments of 10 to 20 percent in the first breeding cycle (Zobel 1977a). Additional gains are expected in future generations, but a gain of 10 to 20 percent appears reliable and defensible.

Tree straightness is desirable, but not easily measured. Straight trees more than pay for themselves when accountants measure harvesting and manufacturing cost advantages and the increased yield as sawtimber is produced. Geneticists report, too, that this goal can be achieved quickly, possibly within one generation of breeding (Zobel 1974).

Another characteristic desired in the South is resistance to fusiform rust. Every analysis stresses importance of progress toward this goal. If trees die, growth and conversion economics become meaningless. But resistant strains are being found and made available for planting in the South (Zobel 1974). Specific gravity of wood can be a significant determinant of pulp yield and processing time in the mill. Moreover, specific gravity increases of 5 to 7 percent have been realized in tree-improvement programs (Ottens and Carlisle 1976).

Revenue gains from tree-improvement programs are measured by comparing additional costs and returns associated with improved planting stock. Only costs or gains over and above those for plantations of unimproved trees are relevant. In practice, additional costs are minimal; in most instances, the only additional or marginal cost goes for improved seeds. Since the economic analysis compares the extra seed costs with discounted values of extra yields at harvest, added expenditures for improved trees are strongly supported. Yield increases of about 5 percent more than justify foreseeable expenditures for seeds (Zobel 1974). Ottens and Carlisle (1976) found that seed costs could be 10 times greater than current rates and still promise profits over a typical rotation. Similarly, it was shown that discounted gains in revenue exceeded current costs of seed production by a multiplicative factor of 4 to 70, depending upon price and yield assumption. In every case, results implied an underinvestment in tree improvement.

Other economic analyses focused on present net worth or internal rate of return as criteria for evaluating tree improvement. Except at abnormally high discount rates, present net worth of investments in tree improvement proved profitable (Dutrow and Row 1976). Internal rates of return were favorable too. Most studies reported rates exceeding 10 percent, ranging up to about 20 percent (Dutrow and Row 1976, Porterfield 1974). Profits from tree improvement can be traced to nominal cost increments even more than to value gains. The cost of improved trees is only a few dollars more than normal stock, and this cost is incurred only once per rotation Other cost advantages should not be overlooked. For example, acres of forest lands required to supply a mill can be reduced, with associated economies in transportation, management, and harvesting operations. From a national or regional perspective, tree-improvement programs release forested acres for other uses by reducing land required to supply a given amount of wood.

Although results and recommendations are similar, a recent study by Clark Row and myself warrants discussion before we consider the possibility that our chosen path may lead to economic pitfalls (Dutrow and Row 1976).

In our approach, we tried to address the question that haunts economists' efforts to predict dollar returns from improved trees: what is the relative growth pattern of superior trees during an entire rotation? Do superior trees exhibit an early burst of growth and then merely parallel growth rates of normal planting stock? Or, is the early growth advantage of improved trees maintained throughout rotations? Admittedly, these questions will be answered only by time. Our technique offers an improved estimate in the interim.

Equations were derived from data on height, diameter, volume, and survival of unimproved loblolly plantations, and were then modified to show gains made by 8-year-old trees in actual tree improvement programs. Indices of gain were then calculated and inserted in the growth equations for unimproved loblolly plantations to simulate behavior of genetically-improved stock in a plantation environment With growth equations modified to reflect genetic gain, we were able to estimate corresponding economic gains.

Some of the specific measures of gains through use of improved loblolly pine trees are of interest. Height indices or adjustment ratios were calculated and reflected an average gain of 3.5 percent over unimproved stock. In over 50 percent of the genetic trials height gains were at least 2.6 percent, and gains of more than 10 percent were recorded for 17 percent of the trials.

Diameter-adjustment ratios were derived by dividing the average diameter of genetically improved trees by the average diameter of unimproved trees. Tree gains were converted to stand gains by applying the diameter-adjustment ratio to anticipated maximum and mimimum diameters; relative frequencies of basal areas occurring for the enlarged diameters were also calculated. The simulation was run, and notable gains in diameter occurred. Fifty-four percent of the genetic crosses showed diameter growth that surpassed the unimproved trees. Average growth increases were about 2 percent, with almost 20 percent of the genetic crosses exceeding a 10 percent gain over unimproved stock. Survival gains also were estimated and results were similar to gains in height and diameter. Volume estimates, however, required a slight departure from the foregoing procedures.

Volume gains in juvenile trees are not directly proportional to volumes anticipated at harvest for either improved or unimproved trees. Thus, instead of calculating "volume-adjustment factors", we estimated diameters and heights at harvest and inserted these measures into accepted volume equations. Average volume increases were significant, about 12 percent per acre. Over large tracts, 63 percent of the acres of improved trees would exhibit growth rates higher than acres of unimproved trees. Furthermore, 20 percent of these acres of improved trees would display volume gains of more than 30 percent.

As in any economic analysis, we eventually turned to evaluating financial implications of gains expected from improved trees. Present net worth was one of the criteria we used for comparing improved and unimproved trees. About 6 percent of the genetic crosses showed financial gains of up to 150 percent. The average increase in present net worth was almost 30 percent, with a median value of 16 percent. Very few of the genetic crosses indicated returns poorer than unimproved trees.

The estimates can be transformed directly from percentage to dollar gains for private plantation managers. Industrial landowners can expect nearly a 30 percent increase in present net worth. For example, if a forest manager estimates a net worth of his loblolly plantation at $100 per acre, he can increase the estimate by about 30 percent or $30 if he changes to genetically-superior stock. Or, stated differently, he could afford to pay up to $30 more per acre for genetically-improved seedlings.

For large timber-producing regions or ownerships with substantial acreages, gains from tree improvement justify large expenditures in nurseries, orchards, and research to assure even higher productivity. For example, in the three-state area of South Carolina, Georgia, and Florida, loblolly pine plantations occupy about 1,100,000 acres. If through conversion to genetically-improved trees, financial productivity per acre could be increased by 30 percent, extremely large investments in tree improvement efforts, with associated economies of scale, would be justified. Since the forest land base is shrinking, publicly subsidized tree-improvement efforts would enhance wood supplies on those acres retained for commercial production.

POTENTIAL PITFALLS

Before the list of benefits from tree improvement generates absolute confidence in our abilities to meet future wood demands, we need to recognize a few pitfalls. Some financial dangers are commonly recognized, but repetition can do no harm. Other dangers are not so well known, yet cast threatening shadows along future paths of tree-improvement efforts.

A familiar and oft cited note of caution is that improper site selection can erase all promise of gain and cause financial ruin. In most cases, the growth rate forecast for improved trees can be obtained only on good sites. These same sites, incidentally, are capable of supporting high value agricultural crops like cotton and soybeans. So we may find ourselves attempting to market improved seeds that grow well on sites that are no longer available to forestry. It makes little economic sense to invest heavily in producing genetically improved stock for nonexistent acres. We might better prepare for the future by investing more research and development dollars to provide planting stock that grows reasonably well on marginal and even poor sites.

Several years ago, I pointed out that rates of return for cottonwood plantations in the Mississippi Delta offered an excellent investment opportunity relative to other forestry uses. But the investment was poor relative to nonforestry opportunities on those sites; and since then agricultural acreage has expanded and acreage intensively managed for forestry has declined (Sternitzke and Nelson 1970).

Geographic location of the site is another potential problem. The history of tree improvement includes many failures when well-intentioned managers transported seeds or seedlings outside natural geographic ranges. Again, we are confronted with a much-invested, nothing-gained outcome.

Furthermore, we are continually directed to combine our genetically-improved trees with plantation management, including site preparation, planting, and cultural treatment. We are also admonished to select the best available sites if we plan to establish a plantation -- with or without improved trees.

Wood production per acre is highest when we establish plantations of superior trees on good sites and follow proven methods of intensive forest management. The group, consisting of plantations, good sites, and genetically-improved trees, must march together either to financial success or disaster. Designing our tree-improvement programs to be so dependent upon capital intensive management techniques on the most expensive acres may be a mistake.

Costs of establishing and maintaining plantations are escalating so rapidly that companies are beginning to reassess expansion plans. If plantation costs become prohibitive, we may find that our increased production of genetically-improved stock serves a declining market.

Interest rates on funds for long-term investments are rising. Labor costs also have increased dramatically in recent years. In either case, we confront a growing scarcity of productive resources. Existing investment funds, arising from internal or external sources, necessarily dwindle. The net result for forest industry might be continued ideological support for plantations of improved trees but lack of money to establish and maintain them.

Other economic forces add to the restrictions on investment capital. In the South, trends are towards harvesting smaller and younger hardwood and softwood trees, with expanding efforts to utilize the entire tree. Processors cannot sit by and await emergence of plantations of large, clear, and straight trees. Survival in the intervening years necessitates adaptation to existing wood supplies of younger and smaller trees. Utilization of these trees requires substantial capital investments in equipment for harvesting, hauling, and processing. This investment capital may have to be reallocated from planned expenditures on plantations of improved trees. Furthermore, as processors and consumers adapt to the use of entire trees of smaller size, the available supply of wood will dramatically increase and premiums for quality wood from improved trees will fall. Certainly, such bleak prospects do not arise from genetic improvement, but from the widespread reliance on capital intensive forest management, with which tree improvement is closely aligned.

If plantation management is becoming prohibitively expensive, some evidence should be emerging that points to failure to maintain plantations or shortfalls in planned rates of planting. In North Carolina, a number of Forest Survey plots containing pine, including plantations, were harvested between 1964 and 1974. Fifty-eight percent of these plots are now occupied by hardwoods (Boyce and Biesterfeldt 1977). Harvested pine stands in Georgia and Virginia experienced a similar fate; over half have reverted to hardwoods. Most of these stands are not plantations and most are in the hands of small, nonindustrial owners. But, loss of plantations from industrial lands has been reported and is included in the data.

The Southern Forest Institute reports that over 157 million superior seedlings were planted in 1975-1976 (Box 1976). But these seedlings occupy only about 200,000 acres, or 0.1 percent of the commercial forest land in the South. It is estimated that more than 1 million acres east of the Mississippi River would have to be reforested to pine each year just to maintain current percentages of loblolly and slash. We are not meeting this goal; instead, we are planting only about 800,000 acres per year and only about 25 percent of these acres receive improved planting stock.

Thus, data suggests that many of our pine forests are reverting to hardwoods and our rate of planting is insufficient to maintain existing percentages of pines. The culprits, in my opinion, are escalating costs and growing scarcity of capital. Small private landowners do not have the money or inclination to invest in intensive forest management. A growing percentage of industry representatives are making expensive adaptations in harvesting, hauling, and processing to accomodate available wood supplies. With limited capital, industry is finding that circumstances often suggest greater profits through adapting to the forest resource rather than investing so heavily to alter it.

This may seem a depressing note to conclude on, but I feel that these are realistic considerations that offer opportunity as well as consternation. I am merely suggesting that risks are inherent in an alliance of so great a proportion of our tree-improvement efforts with the most expensive forest management regimes. We might realize greater long-run benefits by seeking ways to increase or just maintain acceptable growth rates on poorer sites with less intensive management. Insuring natural regeneration of chosen stock, relying very little on fertilizer application, and developing trees that compete efficiently and produce added wood fiber appear to be research goals that would pay off in terms of enhanced wood supplies. I applaud and am awed by progress in genetic improvement, but feel constrained to point out some economic factors that urge us to align our improved trees with less costly management companions.

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THE GENETIC AND ECONOMIC EFFECT OF PRELIMINARY[1] CULLING IN THE SEEDLING ORCHARD

Don E. Riemenschneider[2]

ABSTRACT.--The genetic and economic effects of two stages of truncation selection in a white spruce seedling orchard were investigated by computer simulation. Genetic effects were computed by assuming a bivariate distribution of juvenile and mature traits and volume was used as the selection criterion. Seed production was assumed to rise in a linear fashion to maturity and then remain constant for the life of the orchard. Expected seed production was used to compute the number of acres that could be planted and volume gain over this acreage was estimated using predicted response to selection and white spruce volume tables. The added volume was compared to the cost of the orchard using the cost-price investment criterion. The cost-price of the volume gain was found to vary little over reasonable intensities of preliminary culling and the optimum intensity remained the same regardless of the juvenile-mature correlation.

Many economic analyses of forest tree improvement projects have already been done (Dutrow 1974). To date, however, most of these studies have dealt with clonal seed orchards (Davis 1967, van Buijtenen and Saitta 1972, Porterfield 1974) rather than seedling seed orchards. I began this study to investigate the genetic and economic potential of a white spruce seedling seed orchard by means of computer simulation. The goals were to determine (1) the effect preliminary culling had on genetic gain and economic return, and (2) the optimum level of culling.

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METHODS

A 4.5 acre white spruce (*Picea glauca* (Moench) Voss) seedling seed orchard in north-central Minnesota was used as the model population. The orchard initially contained 7,200 individuals representing 239 open-pollinated families. Early measurements of height growth and estimates of heritability have been reported (Mohn *et al*. 1975).

Although combined family and mass selection is likely to be more efficient, the problem was reduced to a manageable level by assuming that there will be two rounds of mass selection in the orchard. Merchantable volume will be the selection criteria. The first round of selection at 15 years after planting will represent juvenile selection or "preliminary culling". The second round of selection will be at 30 years after planting. This final selection will be on the basis of the mature characteristic. Approximately 450 individuals (or 6.25 percent) will remain after all selections have been completed. Gain from parental selection was not considered. A termination date was set at 50 years after planting.

With this culling schedule there will be two productive stages in the life of the orchard. From 15 to 30 years after planting, genetic gain will be the result of the correlated response of the mature trait to preliminary culling based on the juvenile trait. Seed production during this period should be increasing as the trees approach maturity. After final selection at age 30 genetic gain will be based on both rounds of selection. Seed production should reach its maximum and remain constant.

The intensity of preliminary culling will affect response to selection in both stages and total seed production in the first stage. It was necessary to quantify this effect and then determine the intensity that maximized the potential return on the orchard investment.

The genetic effect of preliminary culling were evaluated by assuming that the two selection criteria are bivariate normally distributed. The technique used in this study has been described by Brown (1967) and applied to a tree improvement problem by Namkoong (1970). The genetic effects of selection were computed as follows:

Let: u = the mature trait and

v = the correlated juvenile trait.

Assume that u and v are bivariate normal with phenotypic correlation r_p genotypic correlation coefficient r_a, and heritabilities h_u^2 and h_v^2.

If $x = \frac{u - \bar{u}}{\sigma_u}$, $y = \frac{v - \bar{v}}{\sigma_v}$, and σ_u and σ_v are the phenotypic standard deviations of u and v, then x and y are standard bivariate normal with:

$\bar{x} = \bar{y} = 0$ and,

$\sigma_x^2 = \sigma_y^2 = 1.0$.

The selection procedure in terms of the univariate distribution of x and y will be to discard all individuals where $y<b$ at the preliminary culling and to discard all individuals where $x<a$ at the final selection.

To determine the culling levels, univariate y is divided into 40 intervals, and for each level of culling at $y - b$, the truncation point $x = a$ is obtained, which gives $p\ (a,b\colon r_p) = P$ where:

$p\ (a,b\colon r_p)$ = the fraction of the population retained after truncation of a bivariate distribution, discarding all individuals where $y<b$ and $x<a$, and

P = the portion of the population the breeder wishes to retain after both rounds of selection (6.25 percent).

The gain made in x by truncation selection in y is:

$\Delta G_{x/y} = i_1\ h_x\ h_y\ r_a$ (Falconer 1960)

where: i_1 = the selection intensity in y,

$h_x = (h_x^2)^{\frac{1}{2}}$,

$h_y = (h_y^2)^{\frac{1}{2}}$, and

τ_a = the genotypic correlation between x and y.

Assuming a large population, the selection intensity i_1 is computed by the stochastic relation $i_1 = \frac{Z\ (b)}{Q\ (b)}$

where: $Z(b)$ = the ordinate of $N\ (0,1)$ at $y = b$, and

$Q(b)$ = the standardized univariate normal density function integrated from b to $+\infty$.

$\Delta G_{x/y}$ represents the genetic superiority of seed produced between the preliminary culling and the final selection.

When the final selection is made by truncation at $x = a$, the total genetic gain obtained in x is given by:

$\Delta G_x = i_2 h_x^2$ (Falconer 1960) where: i_2 = the selection intensity in x after truncation selection at $y = b$ and $x - a$, and

h_x^2 = the heritability of x.

The method of computing i_2 is described by Young and Weiler (1961) and a mathematical proof is given by Weiler (1959). The expected mean of x after both rounds of selection ($\bar{x}'$) can be written in terms of a univariate distribution.

$$E(\bar{x}') = \frac{Z(a)\quad Q(A) + r_p\, Z(b)\quad Q(B)}{P}$$

where: $A = \dfrac{b - r_p a}{\sqrt{1 - r^2 p}}$, $\quad B = \dfrac{a - r_p b}{\sqrt{1 - r^2_p}}$, and

r_p = the phenotypic correlation coefficient.

And because the original distribution of x has mean 0, $\bar{x}' = i_2$.

ΔG_X represents the genetic superiority of seed produced after the final selection.

$\Delta G_{X/Y}$ and G_X are expressed as a percent of $\bar{u}$ by multiplying times the coefficient of variation of u.

The amount of seed produced by an orchard is equally as important as genetic gain. Seed production was assumed to begin 15 years after planting and then rise linearly to a constant level of 250 cones/tree/year (Nienstaedt and Jeffers 1970) at 30 years after planting. Total yearly seed production was then computed as the average per tree production times the number of trees in the orchard.

The volume growth in excess of normal yield produced by this improved seed is:

$$V = \frac{A \cdot Vn \cdot G}{100}$$

where: A = the number of acres regenerated based on 8 x 8 foot spacing and 70 percent average seed viability,

Vn = normal yield per acre on medium site land with 40 year rotation (Stiell and Berry 1973), and

ΔG = percent genetic superiority of the seed depending on the stage in which it was harvested.

The schedule of activities that were included as costs are shown below:

Year		Activity
	Selection Phase	
1		Select parents and collect open-pollinated seed
1		Extract and prepare seed
	Nursery Phase	
2		Prepare bed
2		Sow
2,3		Maintain seedbed
4		Transplant
4,5		Maintain transplant bed
6		Lift and wrap stock
	Orchard Phase	
6		Purchase land
6		Prepare site
6		Plant
6-55		Maintain
20		Measure
20		Mark and cull
21-35		Collect seed
35		Measure before final selection
35		Mark
36-55		Collect seed

Estimates of the cost of each activity were obtained from individuals who participated in the project or from organizations that had experience in similar operations. An inflation rate of 4 percent was included when estimating future costs. Costs that occur between 15 and 20 years after planting, especially seed collection, will vary with culling intensity. As culling intensity is increased, these costs are reduced.

The investment criterion used to evaluate culling alternatives was the cost-price relation (Lundgren 1973). This is the price at which a product must be sold in order to break even on the investment. Because output is produced over a period of years, this price was necessarily assumed to be constant. It was computed by dividing cost by output ($/cord) in terms of present equivalents. The present equivalents of cost and output were obtained using standard discounting procedures and an interest rate of 8 percent.

RESULTS

In the Minnesota orchard, heritability for height at 8 years after planting was 0.35 with a coefficient of variation of 34 percent. On the basis of these estimates it was felt that a heritability of 0.30 for volume with a coefficient of variation of 20 percent would provide a conservative estimate of gains from selection.

Seed produced from age 16 to age 30 ($\Delta G_{x/y}$) and from age 31 to age 50 (ΔG_x) were found to be genetically superior (fig. 1 and 2). When levels of culling are low, $\Delta G_{x/y}$ is also small because i_1 is small. But when levels of culling rise, $\Delta G_{x/y}$ also rises appreciably. If all selection is done at age 15, $\Delta G_{x/y}$ is 6 percent, 8 percent, and 11 percent for correlations of 0.5, 0.7, and 0.9, respectively.

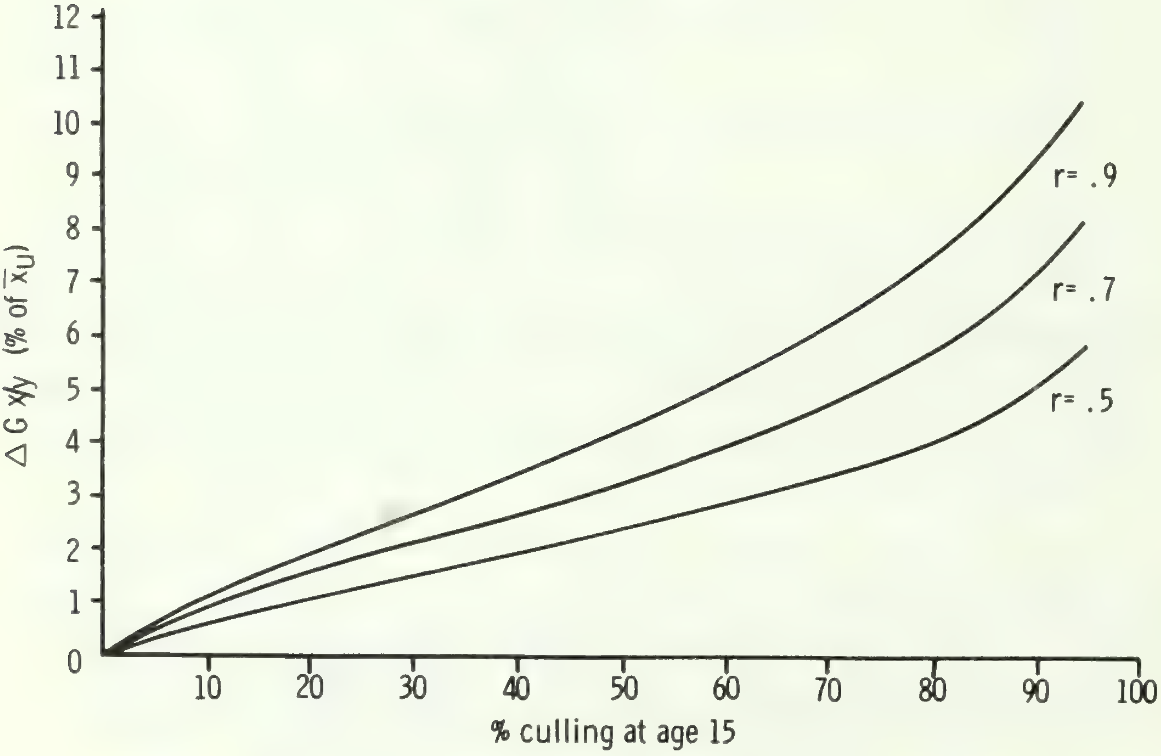

Figure 1.--Gain in the final selection criterion with preliminary culling.

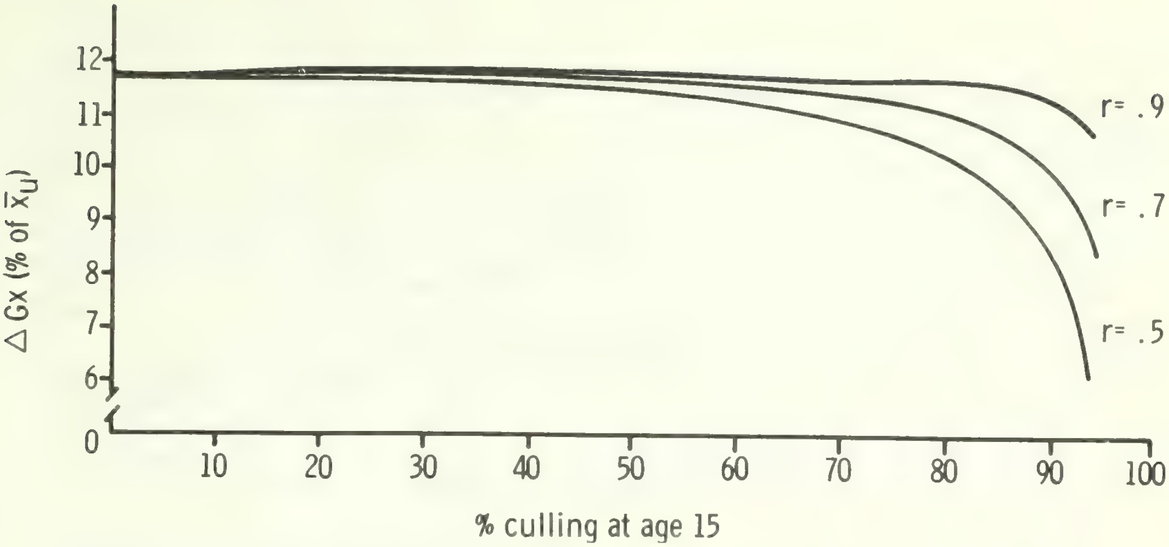

Figure 2.--Gain in the final selection criterion after two rounds of truncation selection.

At low and intermediate levels of culling, ΔG_x does not decrease appreciably. Maximum ΔG_x is 12 percent when $i_1 = 0.0$ for all correlations. For correlations of 0.5, 0.7, and 0.9, ΔG_x is reduced to 6 percent, 8 percent, and 11 percent if all selection is done at age 15. The drop in ΔG_x is not great until high levels of culling are reached and the drop is more severe if the correlation between traits is low. At the maximum culling level $\Delta G_{x/y}$ should equal ΔG_x because there will be no second round selection. The fact that the values obtained agree closely provides a good check on the computational procedures employed.

The present equivalent of the predicted volume in excess of normal yield maximizes at an intermediate point (figs. 3 & 4). This is because the volume gain from pre-final selection seed is a function of both seed production and $\Delta G_{x/y}$, which vary inversely as culling level increases, the curve maximizes at an intermediate point. Because stable seed production is assumed after year 30, only genetic gain after 30 years influences volume gain. The curve decreases slightly at high levels of culling. The importance of early seed production and selection can be seen in the relative heights of the two curves. Although this early production is low, it contributes significantly to the total volume gain when considered for the entire investment period. More volume is produced at higher correlations, but the maximum point is reached at about 50 percent culling.

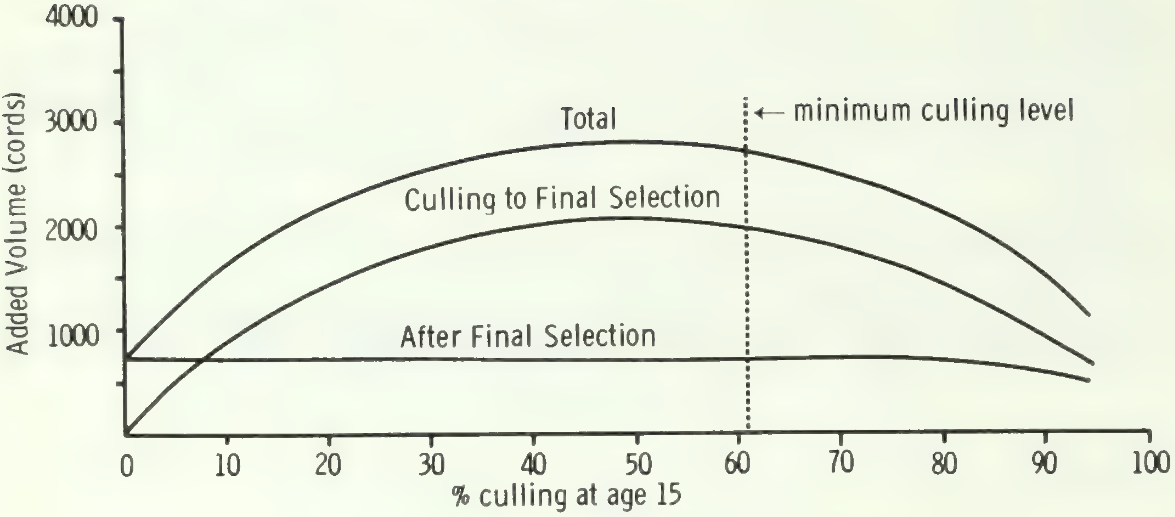

Figure 3.--Gain in volume at rotation age (juvenile-mature correlation = .7) (present equivalent).

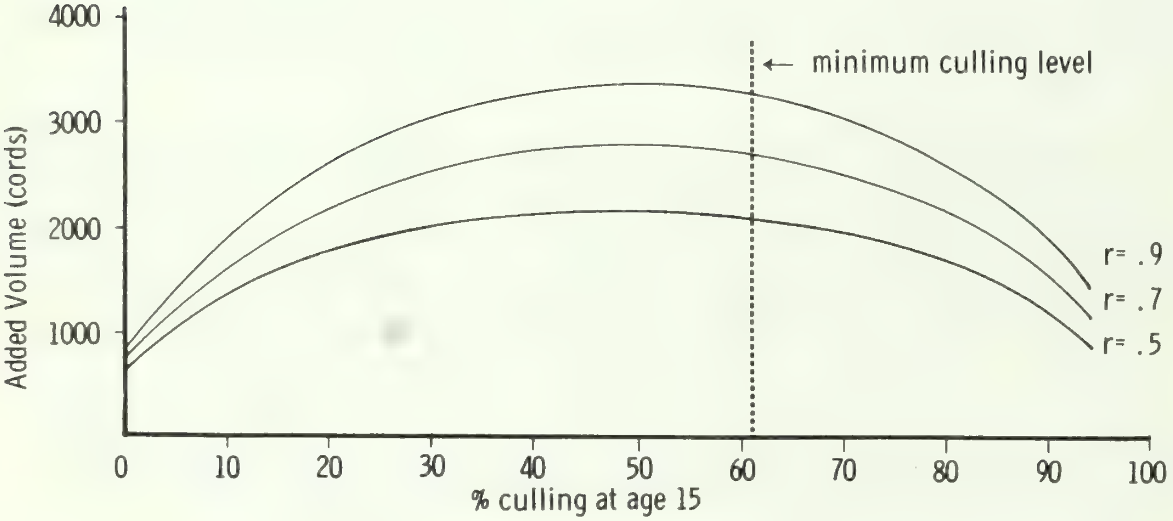

Figure 4.--Total gain in volume at roation age (present equivalent).

Total orchard seed production was assumed to be a linear function of the number of trees in the orchard. Obviously at low culling levels this linear relation will not exist because crowding will reduce average per tree production. Stocking data (Stiell and Berry 1973) indicate that overcrowding and mortality will occur in the model orchard unless 61 percent of the trees are removed at age 15. This would seem to be the minimum intensity of culling above which volume gain predictions may be accurate.

The present value of costs that are not affected by culling level are shown below:

Activity	Cost
Selection and seed preparation	$ 693.33
Nursery handling	660.39
Land purchase and site preparation	131.80
Planting, maintenance, pre-culling measurements	1,952.30
Seed collection after final selection	2,769.28
TOTAL	$6,207.10

The total present cost ranged from $14,282 at the minimum culling intensity of 61 percent to $8,131 at maximum culling.

The cost price of the gain in volume is a u-shaped curve (fig. 5). The cost/cord is high at low culling levels where $\Delta G_{x/y}$ is small; it reaches a minimum at 73 percent culling and increases at high culling levels because seed production is reduced. Again the curves optimize at the same culling level regardless of the correlation between traits. The minimum price does vary with the correlation coefficient.

The shape of the cost-price curve is flat for the most likely culling intensities. This indicates that a good deal of flexibility is permitted before the cost of production is measurably affected. Also, although the juvenile-mature correlation affects the economic feasbility of the program as a whole, it has little impact on the optimum intensity of preliminary culling.

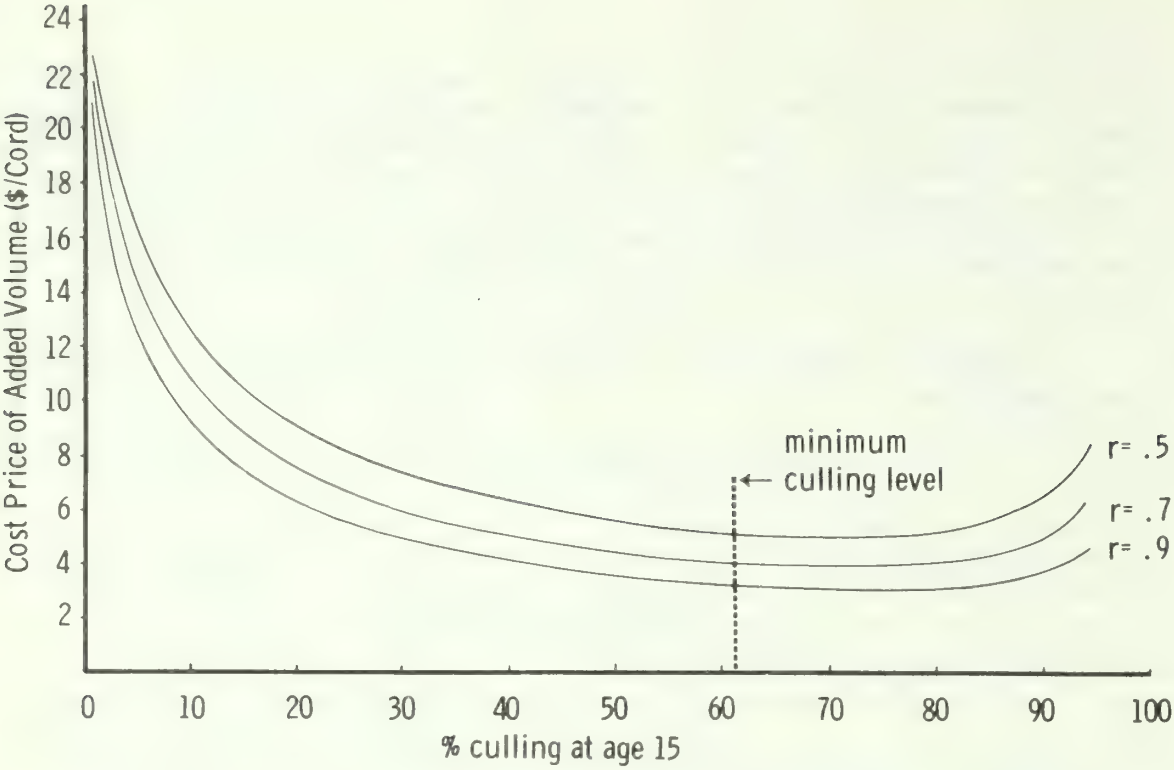

Figure 5.--Cost-price of volume gain.

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DAMAGE TO SOUTHERN MICHIGAN CONIFERS DURING THE WINTER OF 1976-77

Jonathan W. Wright, Donald DeHayes, and Walter A. Lemmien[1]

ABSTRACT.--In southern Michigan, the winter of 1976-1977 was marked by unseasonably cold weather in early December, prolonged cold weather in December and January, severe drought at the onset of cold weather, and by higher than average absolute minimum temperatures. Damage, presumably from the early December cold weather, was severe to southern seedlots of ponderosa pine, Austrian pine from the western Mediterranean, *Cryptomeria*, Spanish origin Scotch pines planted in low-lying areas, and southern seedlots of white fir. Surprisingly, there was little damage to eastern white pine from the southern Appalachians, southwestern white pine from Arizona and New Mexico, baldcypress and *Metasequoia*. Comparisons between laboratory and field experiments indicate that laboratory experiments can give useful information about the temperatures at which appreciable injury can be expected in the field.

The winter of 1976-77 was the coldest in memory for many parts of the Eastern United States. Southern Michigan was no exception. It seemed desirable to assess the damage caused because there is a good possibility that woody plants which survived that winter will continue to thrive for many years.

HOW SEVERE WAS THE WINTER?

The winter was especially severe as regards average temperature, duration of cold weather, and drought. For Lansing, the average December temperature was 11.5°F below the 40-year average, and December had a total of 1,445 degree-days (below 65°F) as compared with normal totals of 1,000-1,100. In Lansing, there was a period of 54 successive days when the temperature did not rise above freezing. Records were also broken in Battle Creek and other southwestern Michigan cities.

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On December 3, 1976, there were unseasonably low temperatures. That night the temperature dropped to -7°F at Lansing and Battle Creek and to -15°F at the Kellogg Forest. Absolute minimums later in the winter were not extraordinary, however. At Lansing the lows were -17°F on December 30 and January 9, as compared with a low of -25°F the previous January 18. At Battle Creek the lows were -10° and -9°F, respectively on December 31 and January 28, as compared with a low of -12°F the previous winter.

The winter was also marked by severe drought conditions. Precipitation had been below normal the previous two years. These drought conditions continued into 1977 and by midsummer were so severe that many small ponds disappeared.

WHEN DID THE DAMAGE OCCUR?

Only for ponderosa pine is it possible to estimate the date on which the damage occurred. For other species it is possible only to say that severe damage was evident by the end of February.

In ponderosa pine, one of us (DeHayes) was in the process of making a detailed laboratory study of cold hardiness. This entailed collecting needles and twigs, freezing them at various temperatures in the laboratory, and measuring electrically the resultant cell damage. Needle collections of nonhardy types made shortly after the December 3 cold spell were mottled. Also, laboratory tests made at the same time indicated cell damage similar to that induced by artificial freezing.

NATURE OF THE DAMAGE

Observations on ponderosa pine indicated that the initial injury to a needle could be at any place, from base to tip. If at the tip, only the tip subsequently became brown. If at the base, the entire needle became brown. Generally, there was a strong correlation between the proportion of needles attacked per tree and the amount of damage per needle.

Cambial injury was less common, and was nearly limited to twigs with 100 percent leaf damage. Some pines were completely brown by mid-February but still retained green cambium and produced new growth later in the spring. Mortality was generally limited to trees which had been damaged in previous years or which were in frost pockets subject to extraordinarily low temperatures.

THE MOST SERIOUSLY DAMAGED SPECIES

Ponderosa Pine (*Pinus ponderosa*)

Damage was most noticeable on the trees of the ponderosa pine range-wide provenance tests established in 1962 at the Kellogg and Russ Forests with O. O. Wells' material. Although these plantations had suffered some damage in previous years, the 1976-77 injury was by far the worst. Damage was nil to the all-interior provenance test established in 1968 with material supplied by the U.S. Forest Service.

In the range-wide tests, trees from California (all parts except the extreme northeast) were hit hardest. Already weakened by cold injury in other years, few seemed likely to survive for more than a year or two. Next worst were trees from Arizona and New Mexico. Most of them seemed destined to survive; their growth rates were already much reduced because of injury in previous years. Trees from the Willamette Valley in western Oregon suffered moderate winter injury (30 to 40 percent of the leaf area brown) in 1976-77 although they had been damaged little in previous years. They had been among the tallest and grew well in 1977 despite their injury.

Ponderosa pines from eastern Oregon, Washington, Idaho and the interior states north of Colorado came through the winter unscathed. According to laboratory tests they had achieved sufficient hardiness even by early December to withstand severe cold.

Another experiment at Kellogg Forest which was a casualty of the cold weather was a plantation of Placerville-produced hybrids which had been planted in the early 1950's. A great number had California ponderosa pine as one parent. Perhaps because they had been planted with better air and soil drainage than found in the provenance test, they had remained thrifty for many years. However, all with California germplasm succumbed after the 1976-77 winter.

In addition to the experimental plantations, Kellogg Forest has four commercial plantations of ponderosa pine which are 35 to 40 years old. They seem to be of Washington or northern interior origin. These were not harmed by the cold although a small percentage of the trees have serious disease problems.

Around the Lansing area and at scattered locations elsewhere, ponderosa pine has been used as an ornamental, and many trees are more than 50 years old. Most of these ornamentals escaped injury.

Austrian Pine (Pinus nigra)

Austrian pine has been a favorite for planting along roadsides in southern Michigan because it is resistant to salt. While disease has been a problem on older trees, damage from cold had rarely occurred on trees south of the Bay City-Muskegon line.

Winter injury was very noticeable after the 1976-77 winter, however. In the range-wide provenance test established in 1961 at Kellogg Forest, most trees from Corsica and southern France had 60 to 70 percent of the foliage turn brown. They had been similarly injured in the nursery but had suffered only minor damage in recent years.

Seedlots from Spain, other parts of France, the Greek Islands, and the Greek Peloponnesian Peninsula were damaged on 10 to 30 percent of their foliage. Trees from Austria, Yugoslavia, northern Greece, Turkey, and the Crimean SSR were not hurt.

Many non-experimental roadside trees, most of them thought to be of Austrian origin, were also damaged. It was typical to find heavy injury (50 to 75 percent of the foliage brown) on one or two of a group of 10 trees, with no injury on the remainder. The damaged trees grew normally during 1977.

White Fir (Abies concolor)

At both Russ and Kellogg Forests we have provenance tests including seedlots from the Rocky Mountain portion of the range. The Russ plantation, on a low-lying site, was damaged most heavily. In the most sensitive seedlots, 100 percent of the leaf area was injured at Russ as compared with 30 to 40 percent at Kellogg.

There was an interesting contrast in hardiness between two Arizona seedlots originating 1° latitude and 500 ft elevation apart. The most severely damaged seedlot in the experiment was the fastest growing one, No. 2427, from an elevation of 8,100 ft and a latitude of 32° 27'N on Mt. Lemmon in extreme southern Arizona. There was very little damage to moderately fast growing seedlot No. 2423, collected from an elevation of 7,600 ft and a latitude of 33° 20'N. Other seedlots from central Arizona and southcentral New Mexico suffered slight to moderate damage (10 to 30 percent of leaf area injured). Slowly growing trees from farther north suffered no damage.

The California-Oregon provenance test organized by W. J. Libby is also represented by a small plantation at the Kellogg Forest. Practically the entire population from these states exhibits introgression from grand fir (Abies grandis), which is a lower elevation and less hardy species of the Pacific Northwest. Trees in this experiment had suffered some winter injury in most previous years, but not to the same extent as in the winter of 1976-77 when they became red-brown.

White fir suffered less permanent damage from the cold than did the pines. The most badly damaged trees from Arizona and New Mexico grew as well in 1977 as in previous years. Even many of the California trees which were red-brown at the end of the winter produced new shoots in the spring.

Eastern White Pine (Pinus strobus)

In southern Michigan, eastern white pine from the southern Appalachian Mountains holds special promise. It has grown rapidly for 18 years and is recommended for commercial planting. We were apprehensive as to the effect of the extreme cold weather on the fast growing seedlots. In three widely separated plantations south of Lansing there was no winter injury, even to trees from northern Georgia. We have not had a chance to re-examine a 10-year-old plantation of southern Appalachian trees located in the northern half of the Lower Peninsula.

The long winter was, however, an extraordinarily hard one for eastern white pines located along roads throughout the Lower Peninsula. Apparently most of the damage is due to blowing salt dust, rather than spray. Where there was considerable open space next to the road, as along a thruway, there was serious needle burn on trees 200 to 300 ft to leeward of the road. In the case of roads bordered by trees, damage was usually limited to within 50 ft of the roadway. Whereas in previous years such damage was usually confined to young trees, some 70-80 ft specimens were brown after the 1976-77 winter. Trees away from roads were not affected, even though in the open.

Southwestern White (Pinus strobiformis) and Limber Pines (P. flexilis)

Southwestern white is a 5-needled pine native to Arizona, New Mexico, and a small part of Texas. It has thick, blue-green foliage, grows at moderate rates, and has been in much demand for Christmas tree planting in recent years. Even the fastest growing seedlots from Texas came through the winter unscathed at both the Russ and Kellogg Forests. Also, older trees in a Battle Creek arboretum were undamaged by the winter.

Limber pine is a slow growing relative from Colorado, Utah, and north. Peculiarly, it suffered apparent winter injury. On a very small number of trees, 30 to 40 percent of the foliage was brown at the end of the winter.

Western White Pine (Pinus monticola)

Western white pines of north Idaho origin were planted at Kellogg Forest and at the Tree Research Center on the MSU campus in East Lansing in 1970. They appeared hardy until the winter of 1976-77 when most of the trees on the MSU campus were severely injured (60 to 90 percent of the needles brown). At Kellogg Forest, damage was severe for trees planted within 10 ft vertical distance of the bottom of a ravine but slight for trees planted on a hilltop or on upper slopes.

Scotch Pine (Pinus sylvestris)

Interracial hybrids of Scotch pine have been planted on hilly ground at Kellogg Forest since 1970. In the plantations there are 50 ft elevational differences within relatively short distances. There are some low spots without air drainage. Within 1 ft vertical distance of these low spots, some trees died. Trees in other parts of the plantations suffered no injury.

Scotch pine of Spanish origin has been recommended for Christmas tree planting in those parts of the state with an average January temperature of 20°F or above, or roughly in the southern third of the state. These recommendations will have to be changed because even in those areas some plantations suffered severe needle injury during the 1976-77 winter. Damage was most serious in low-lying areas. In some cases nearly 100 percent of the needles were brown and it appeared that mortality would result. We have not had a chance to evaluate the long-term effects of the damage in plantations with less severe injury.

Sugi (Cryptomeria japonica)

Cryptomeria or sugi is a Japanese conifer which is more accustomed to a Tennnessee than a Michigan climate within its native range. Nevertheless, we have two specimens which have lived for more than 40 years on the MSU campus. One, situated about 10 ft from a tall building escaped serious injury. On the other, situated in the open, more than half of the leaf area was dead by the spring of 1977.

SOME SURPRISING ESCAPES

In view of the severity of the winter, we were not surprised as much by the presence of brown trees in some species as by their absence in others. Douglas-fir is a case in point. At Russ and Kellogg Forests there are provenance tests covering the entire interior portion of the range and one seedlot from western Oregon. These tests were planted from 1965 to 1968. Although late spring frosts had killed newly expanded shoots in several years, there had been no previous winter injury. Nor was there any winter injury following the 1976-77 winter, even to fast growing seedlots from southern Arizona and western Oregon.

Metasequoia is a fast growing conifer from a remote part of China. Charleston, South Carolina is the American city having the climate most similar to that prevailing in its native valley. Only unbounded optimism would have caused people to plant it as far north as Michigan in the first place. However, there was only a slight amount of twig dieback--no more than in previous years--on the several trees which have been planted on the MSU campus. This was true in spite of the fact that all had been planted in exposed situations.

Baldcypress (*Taxodium distichum*) was another surprise because its native range extends only as far north as southern Illinois and southern Indiana. We have three old trees on the MSU campus, none planted in a particularly favorable spot. They were just as healthy after the 1976-77 winter as in any other year.

First-generation hybrids between Austrian and Japanese red pines (*Pinus densiflora*) have been planted at several places in southern Michigan during the past 10 years. They did not suffer any noticeable winter injury even though needles turned brown on some Austrian pines similar genetically to the parents of the hybrids.

CONCLUSIONS FROM THE WINTER

The unseasonably cold weather in early December presumably was responsible for most injury suffered by nonhardy types of ponderosa and Austrian pines. For those species the hardening pattern was such that trees could not withstand low temperatures so early in the season although they withstood even lower midwinter temperatures in previous years. The hardening pattern is not the same for all species, however. For example, forsythia, quince, and several rhododendrons flowered profusely in 1977 although their flower buds had been killed by January cold a few years earlier. Thus, the winter of 1976-77 was a good one to test hardiness in some species, and not a good one in others.

Waiting for an abnormally cold winter is a slow way to select trees for cold hardiness. For that reason, laboratory experiments have been undertaken to determine artifically the temperatures at which freezing injury occurs. Three such experiments performed on provenance test material growing at the Kellogg Forest near Battle Creek provide data applicable to southern Michigan. They are the eastern white pine experiment by Maronek and Flint (1974), the unpublished study of black cherry by Sung Gak Hong of the University of Minnesota (now of the Republic of Korea) and the PhD. thesis work on ponderosa pine by one of the present authors (DeHayes). In eastern white pine, needles of the least hardy types were injured severely if subjected to laboratory temperatures of -25° to -44° (-31° to -42C) from November to January; field-grown trees did not experience such low temperatures and suffered no injury. In black cherry, laboratory temperatures of -40°F (-40C) in January caused twig damage to the least hardy types; field-grown trees did not experience such temperatures and suffered no damage. In ponderosa pine, laboratory determined damaging temperatures in early December were much higher for California trees, slightly higher for Arizona-New Mexico trees, and slightly lower for Washington trees than the actual low temperature of -15°F (-26C) recorded at Kellogg Forest on December 3. Damage was great for California trees, moderate for Arizona-New Mexico trees, and nil for Washington trees.

Thus, it appears that the laboratory tests of hardiness provide useful information about the temperatures at which appreciable field damage can be expected.

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PERFORMANCE OF NORTHERN WHITE-CEDAR IN CENTRAL ILLINOIS

J. J. Jokela and C. L. Cyr[1]

ABSTRACT.--Growth and survival of 20 provenances of northern white-cedar in the nursery and to age 12 in 3 test plantings in east central Illinois were examined. Survival at age 12 exceeded 95 percent in all tests. Total height differed significantly among provenances at age 4 in the nursery and at greater ages in all tests except after the first and second growing seasons following extensive and severe foliage injury during the winter of 1970-71. Height rankings of provenances varied between test sites and with age on the same site. Provenances from isolated occurrences south of the main range of the species were shortest at age 12. Lack of a well defined geographic pattern of variation may reflect the influence of localized lowland and upland ecotypes. The excellent performance of the species in all tests supports its use for a variety of types of barrier and shelter plantings.

Northern white-cedar (Thuja occidentalis L.) is widely distributed on a variety of lowland and upland sites in southern Canada from Manitoba to Nova Scotia and in the United States and northeastern Minnesota, northern and eastern Wisconsin, northern and central Michigan, New York, and northern New England. It occurs locally in Illinois, Indiana, Ohio, southern New England, and in the Appalachian Mountains from western Pennsylvania to eastern Tennessee and western North Carolina. Its occurrence in Illinois is limited chiefly to bluffs and cliffs of St. Peter sandstone in extreme northeastern portions of the State and occasionally to rock outcroppings along the Illinois River in LaSalle County. From an 1853 record, it is known to have occurred as far south as Peoria (Jones 1963).

The first range-wide provenance study of northern white-cedar was initiated by Scott S. Pauley in 1964 when he obtained seed collections from 32 stands located throughout the botanical range of the species.

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Seed of various provenances was sown in nurseries in Illinois, Michigan, Minnesota, and Wisconsin for the production of planting stock for tests in these States under the North Central Regional Project NC-51 (currently NC-99).

Early results from these studies suggested to Wright (1976) that northern white-cedar was genetically uniform throughout its range. In contrast, Jeffers (1976) found significant height differences among provenances in a northern Wisconsin and a western Upper Michigan planting 9 years old. He concluded that genetic variation does exist in the species, at least in terms of height growth. On the basis of his finding of no significant differences in the nursery and those of Wright, he speculated that genetic differences may not be expressed when trees are grown under optimum conditions.

This paper reports on the performance of 20 provenances through age 12 in Illinois.

MATERIALS AND METHODS

Three field tests were established in east central Illinois with planting stock raised in the Mason State Tree Nursery, Havana, Illinois. Twenty seed lots were stratified in moist sand at 36-40°F for 40 days prior to being sown on April 11, 1965. The seedbeds were mulched with 1 to 2 inches of well rotted sawdust and maintained as a regular production bed. Germination and yield of 2-0 seedlings varied greatly among provenances; however, these differences were not measured because the quantity and undoubtedly the quality of seed sown varied among provenances. The seedlings were lifted and transplanted into regular nursery beds in a randomized complete block design with three replications on May 17-18, 1967. Total heights of 10 transplants in each plot were measured to the nearest .05 feet before lifting in April 1969.

A 3-row windbreak was established with 2-2 bare root transplants on Drummer silty clay loam (Typic Haploquoll) in the Illini Forest Plantations, Urbana, in April 1969. Trees were planted 6 feet apart in rows spaced 9 feet apart. Each of the 20 provenances was represented by a 6-tree plot in two rows oriented diagonally across the break in each of four replicates. The remaining nursery stock was planted in a nearby holding plot.

A second test, a 3-row audio-visual screen, was established in April 1970 with 2-2-1 stock with intact soil balls, on Sidell silt loam (Typic Argiudoll) and Flanagan silt loam (Typic Aquiargiudoll) on the University Veterinary Research Farm located one-third mile east of the first test. Trees were planted 10 feet apart in the two outer rows and 5 feet apart in the middle row. Rows were spaced 8 feet apart. Each provenance was represented by a 4-tree plot--a row of three trees oriented diagonally across the screen plus an additional tree in the center row at 5 feet spacing. The provenances occurred in up to six replicates if stock was available. Data for only the 17 sources that occurred in the first five replicates (the sixth replicate was destroyed by herbicidal drift from an adjacent field) are reported herein.

The stock remaining in the holding bed was planted as 2-2-2 transplants in April 1971 in a visual screen at the Vermilion River Observatory located approximately 30 miles east of Urbana. The soil, a Vance Silt Loam (Typic Hapludalf), is a timber soil in contrast to the prairie soils of the other tests. Trees were planted with intact soil balls around their roots. Various numbers of trees of 16 provenances, totaling 264, were planted completely at random at a 7-foot spacing in an outer row of a multi-row planting.

Weeds were controlled by mulching or disking the first growing season and subsequently by one or two mowings annually.

Total heights of surviving trees were measured annually except after the first growing season in the Veterinary Research Farm Test, and at ages 9 and 11 in all field tests.

RESULTS AND DISCUSSION

Survival

Tree survival at 12 years of age averaged 99, 98, and 96 percent in the Illini Forest, Veterinary Research Farm and Vermilion River Observatory plantings, respectively. All the mortality was attributed either to pilferage or mowing accidents, so it can be concluded that all provenances survived equally well. Sporadic bagworm infestations have been sufficiently severe on occasional trees to suggest that bagworms might cause lasting crown injury or death. All trees survived the record drought of 1976 and 1977 without apparent injury.

Winter Injury

The foliage of northern white-cedar is subject to winter injury in Illinois. The most severe injury observed in the test plantings occurred during the winter of 1970-71 when most trees in the Illini Forest Plantation incurred some degree of injury and 30 percent lost at least half their foliage. Severity of injury showed no definite geographic pattern. The most severely injured provenances were southern Ontario (UMN 33), northeastern Vermont (UMN 17), and Illinois (UMN 34). The least severely injured provenances were central Minnesota (UMN 18), northern Ontario (UMN 40), and western Upper Michigan (UMN 32). Winter injury was much less extensive on the better drained, more exposed site on the Veterinary Research Farm. In subsequent years, only minor, isolated instances of winter injury have been noted except during the winter of 1976-77 when most trees in the Vermilion River Observatory test suffered light to moderate injury. The buds were not injured, so all trees recovered.

Total Height

Total height growth in the test plantings has equaled or exceeded that of red, white, and Scots pine on adjacent sites at comparable ages. Contrary to earlier results from tests in the Lake States, significant differences were found at 4 years of age in the nursery and at greater ages in field tests. These significant differences occurred under near optimum growing conditions, but they were obscured after the first and second growing seasons following the winter of 1970-71 when winter injury was unusually severe (table 1).

Table 1.--Significance of differences in total height among provenances

Plantation	Age (years)						
	4	5	6	7	8	10	12
Nursery	**	-	-	-	-	-	-
69-2	-	**	**	NS	NS	*	**
70-4	-	-	-	NS	*	**	**
71-1	-	-	-	-	**	**	**

* Significant at .05 level of probability.
** Significant at .01 level of probability.

Although significant differences were found, ranking of provenance means varied from test to test. Simple correlation coefficients, computed from provenance means at age 4 in the nursery, age 2 in three central Illinois tests and age 9 in a Wisconsin and a Michigan test (Jeffers 1976), are low to moderatly high (.19 - .77) (table 2).

Ranking also varied with age in the same plantation. Changes in rank reflect varying seasonal growth effected by varying environmental factors favoring or disfavoring certain genotypes. A season's growth is a major component of total height at young ages and may be large relative to real differences among provenances, so early results from provenance tests may be less reliable than they are often purported to be. This is illustrated by the change in the relative ranking of two Ontario sources (fig. 1). Trees from northern Ontario source

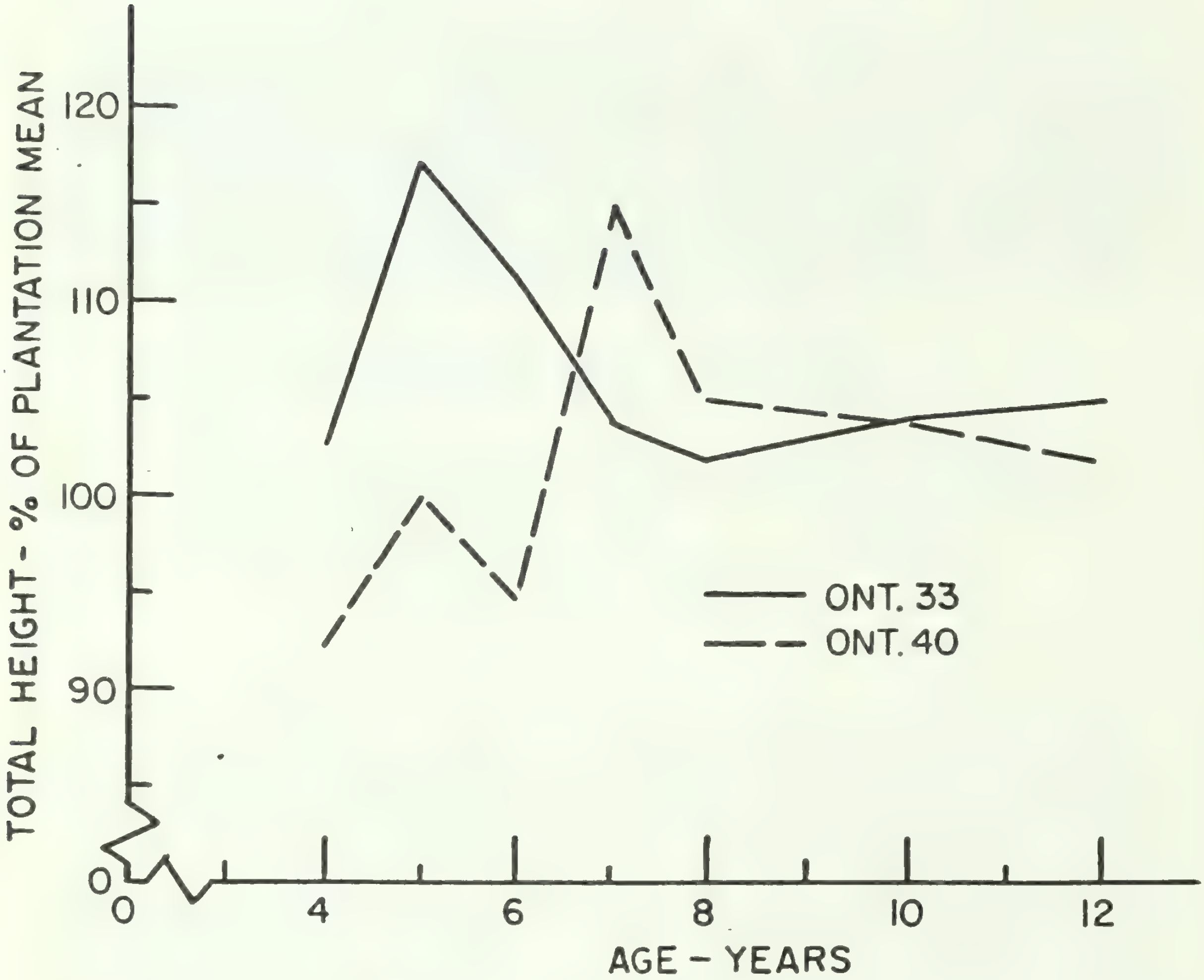

Figure 1.--Relative ranking of provenances with the least (Ont. 40) and the most (Ont. 33) foliage during the winter following the sixth growing season (Illini Forest Plantations).

(UMN 40), which incurred the least foliage injury in the Illini Forest Plantation during the winter of 1970-71 and had previously been one of the slowest growing, was the second tallest after the 1971 growing season. Trees from the southern Ontario source (UMN 33) were the most severely injured.

Table 2.--Between plantation correlations in mean height of provenances expressed as simple correlation coefficients with significance levels

	Nursery (age 4)	69-2	70-4	71-1	Wisconsin
Illinois (age 12)					
69-2	.77*				
70-4	.22	.57**			
71-1	.68**	.73**	.62**		
Wisconsin (age 9)	.20	.40*	.19	.20	
Michigan (age 9)	.26	.49*	.21	.48*	.55**

* Significant at .05 level of probability.
** Significant at .01 level of probability.

Provenance means at age 4 in the nursery and at age 12 in the three field tests, expressed as a percentage of the plantation mean, are given in table 3. Provenances from Washburn County, Wisconsin (UMN 29), Grand Isle County, Vermont (UMN 28), Shawano County, Wisconsin (UMN 21), and Chippewa County, Michigan (UMN 31) were generally the tallest. The first two were among the fastest growing and the last two were average in tests in northern Wisconsin and western Upper Michigan (Jeffers 1976). The slowest growing provenances were from Kenora District, Ontario (UMN 35), Bland County, Virginia (UMN 19), Kane County, Illinois (UMN 34), and Annapolis County, Nova Scotia (UMN 38). The lack of a definite geographic pattern of variation in growth rate and susceptibility to winter foliage injury may reflect the existence of localized lowland and upland ecotypes described by Habeck (1958) and Musselman, Lester, and Adams (1975).

The excellent survival and growth of northern white-cedar in the test planting encourage greater use of this species in Illinois. The dense evergreen foliage and compact crowns create tidy, attractive, living barriers. It would be particularly useful for audio or visual screens, windbreaks, and wildlife cover plantings where space is at a premium.

Table 3.--Relative height of provenances of northern white-cedar in the nursery at 4 years and in three Illinois plantations at 12 years of age

UMN	Seed origin				Plantation			
source no.	County	State or Province	Lat.	Long.	Nursery	69-2	70-4	71-1
			(deg.N)	(deg.W)	(% of plantation mean)			
19	Bland	VA	37.1	81.1	83	92	93	82
34	Kane	IL	42	88.2	97	93	99	--
37	Herkimer	NY	42.9	75.1	118	105	96	--
33	Blandford Twp.	ONT.	43.3	81	112	105	101	--
36	Clinton	NY	44.6	73.7	95	98	107	97
28	Grand Isle	VT	44.6	73.3	113	103	105	111
21	Shawano	WI	44.6	88.4	105	103	106	115
17	Orleans	VT	44.7	72.0	100	98	96	97[1]
38	Annapolis	N.SCOT.	44.9	65.2	85	90	94	93
30	Somerset	ME	45.6	70.3	106	99	97	95
22	Forest	WI	45.8	88.9	92	102	103	98
29	Washburn	WI	46	92	107	105	111	108
23	Forest	WI	46.0	88.9	98	99	97	97
31	Chippewa	MI	46.3	84.2	105	104	107	108[1]
18	Itasca	MN	47	93	103	99	--	--
32	Houghton	MI	47.1	88.6	104	100	97	92
16	St. Louis	MN	48.0	91.6	103	96	--	--
39	Frost Twp.	ONT.	49.5	84.7	108	103	97	111
40	Gurney	ONT.	49.5	82.2	92	102	107	98[1]
35	Kenora Dist.	ONT.	51.5	90.3	80	94	--	--
Mean (meters)					.40	3.02	3.02	1.86
Probability of >F					<.005	<.01	<.001	<.005

[1] Based on less than 15 observations.

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GEOGRAPHIC VARIATION OF JACK PINE (PINUS BANKSIANA LAMB.)[1]

Jung Oh Hyun[2]

ABSTRACT.--Ten traits were measured on 10-year-old jack pine grown at Cloquet, Minnesota, from seed collected from 90 provenances. The traits were examined by using analysis of variance and computing correlations for all combinations of 9 traits plus latitude, longitude, and elevation of the seed sources and cluster analyses using the D^2 values from the Mahalanobis distance function. Results of the ANOVA showed that seed sources differed greatly for the 10 traits measured and results of the cluster analysis showed that populations can be geographically defined.

Jack pine (*Pinus banksiana* Lamb.) is an important conifer in North America. It is abundant, grows well on drier, sandy soils, has rapid early growth, and is suitable for pulp and solid wood products. Its range extends from northern New England and the Maritime Provinces west to the Lake States, Alberta, and the Mackenzie District of Northwest Territories.

Because of its importance in Minnesota, a provenance study was begun in 1940. Geographic variation among provenances in this test was reported by Schantz-Hansen and Jensen (1952, 1954) and Schoenike *et al.* (1959). An additional test was begun in 1951 by P. O. Rudolf and several reports on this experiment have been published (Stoeckeler and Rudolf 1956, Conover 1957, Arend *et al.* 1961, Batzer 1961, Rudolph 1964, King 1965, King and Nienstaedt 1965, and Alm and Jensen 1969. Schoenike (1962, 1976) did a detailed study of jack pine variation in natural stands and reported large amounts of variation in many traits; some characteristics showed variation patterns related to geographic location. A range-wide provenance study was undertaken by Holst and Yeatman (1961) and Yeatman (1964, 1966). Yeatman (1966) found an overall clinal pattern of genetic variation resulting from environmental adaptation. The material from the Holst-Yeatman study was widely distributed within the species range; a test in Minnesota is the basis for this report. It is the most recent and comprehensive jack pine provenance test in Minnesota and was planted in 1966. The objectives of study were to (1) examine the variation among seed sources for a number of morphological traits and (2) examine the pattern of this variation in relation to geographic distribution using cluster analysis.

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MATERIALS AND METHODS

In May of 1966, 1-1 stock from 90 seed sources were planted at Cloquet, Minnesota (fig. 1). A randomized complete block planting design was used with 4 tree-row plots and 5 replications.

When the trees were 10 years old from seed, the following measurements were taken: (1) total tree height, (2) tree diameter at 1 foot above the ground, (3) bark thickness at 1 foot above the ground, (4) crown width, (5) average number of live branches per whorl, (6) average branch angle, (7) average cone angle, (8) cone serotiny, (9) cone abundance, and (10) type of cone curvature. Measurements were made on the first two living trees in each plot.[3]

Standard Analysis of Variance was used to evaluate all of the traits measured except type of cone curvature. (The nature of the cone curvature data made it unsuited for analysis of variance.) Missing data were handled using the procedures given by Snedecor and Cochran (1972) because less than 2 percent of observations were missing.

Differences due to geographic variation were estimated for the nine traits from the ANOVA table by:

$$\frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2}$$

where σ_G^2 = component of geographic variance,

σ_E^2 = component of environmental variance.

Simple correlation coefficients were computed for every possible pair of 12 variables: 9 traits (as previously listed excluding the type

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[3] Details on measurement techniques can be found in "Geographic variation of jack pine (Pinus banksiana Lamb.)" by J. O. Hyun (1976) on file at the Library, College of Forestry, University of Minnesota.

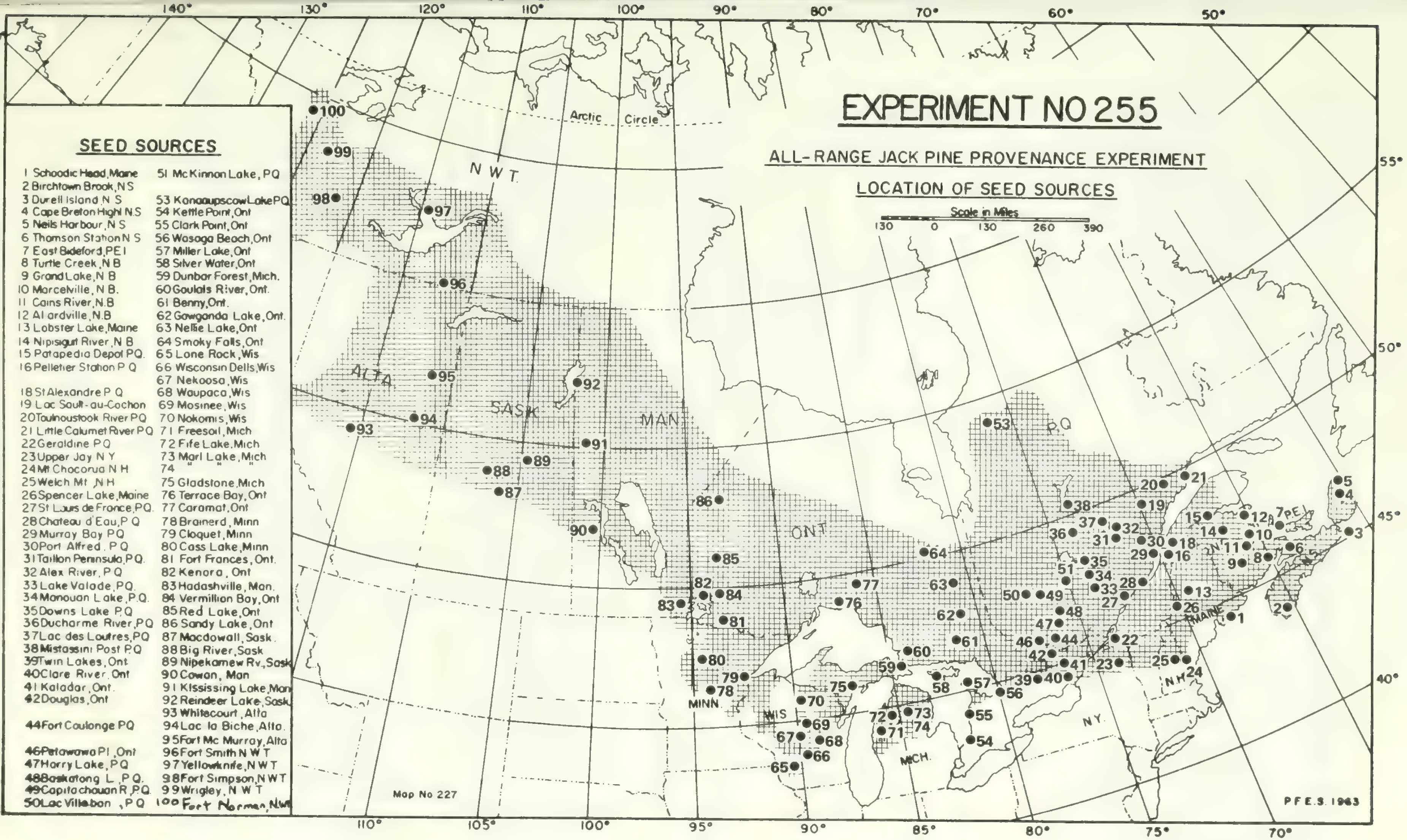

Fig. 1. Natural distribution of jack pine (shaded) and seed sources included in this study (numbered dots). This map was modified from the Map No. 227 for Experiment No. 255 of the Petawawa Forest Experiment Station.

of cone curvature) and 3 geographic gradients (latitude, longitude, and elevation).

The data were fitted to the multivariate analysis using the generalized distance function of Mahalanobis (1936) as treated by Schoenike (1976), Rose (1974), Squillace (1966), Wells (1964), and Wright and Bull (1963). The multivariate analysis made it possible to treat all the traits simultaneously and to compare each seed source with every other one. The formula for generalized distance when more than two traits are compared is:

$$D^2=\Sigma_i\Sigma_j \; S_{ij}{}^{-1} d_i d_j$$

where

D^2 = generalized distance,

d_i = the mean population distance for the ith variable,

d_j = the mean population distance for the jth variable, and

$S_{ij}{}^{-1}$ = the element in the inverse of the covariance matrix corresponding to the ith and jth variable.

D^2 values were computed for the 10 traits measured from the trees from the 90 seed sources[3]. The D^2 values were then used in a cluster analysis to develop numerical values expressing the relative similarities among seed sources.

RESULTS AND DISCUSSION

Significant differences (5 percent or 1 percent level) were found among seed sources for all traits except number of live branches per whorl (table 1). The geographic location of the seed source had the most effect on height, diameter, bark thickness, and crown width; had a moderate effect on cone angle, cone abundance, cone serotiny, and branch angle; and had the least effect on number of live branches per whorl.

King (1965) showed that the seed sources best suited for the Lake States are found within the region. However, results from our study show that height growth of three seed sources from Ontario (42, 55, and 60), three seed sources from Quebec (33, 47, and 48), and one from Manitoba (83) exceeded the local source (79). Therefore, in jack pine breeding, seed sources from other regions can be included in addition to local sources.

Height, diameter, bark thickness, and crown width are highly and positively correlated to each other (table 2). Furthermore, these four traits show moderate negative correlation with latitude. Only diameter and crown width show significant (1 percent level) negative correlation with longitude. No traits have a significant correlation with elevation. The number of live branches per whorl show a small but significant negative correlation with longitude. A significant, negative, correlation was determined between cone serotiny and cone abundance and a significant, positive correlation between serotiny and longitude. Schoenike (1976) found a significant, positive, correlation between serotiny and latitude, but I could not demonstrate this relation.

Table 1.--Summary of field measurements and analysis of variance

Traits	Plantation mean	Standard deviation	Range of seed source means	F ratio seed source/error	Proportion of geographic variation
					percent
Height	12.8 ft.	1.55 (12)[1]	6.3-16.0	7.05**[2]	55[3]
Diameter	3.2 in.	.41 (13)	1.4- 4.2	6.34**	52
Bark thickness	21.5 $\frac{1}{10}$in.	3.12 (15)	8.3-33.5	8.54**	60
Crown width	9.7 ft.	1.27 (13)	3.9-12.2	5.74**	49
Branch angle	61.0°	6.42 (11)	46.1-72.6	2.28**	30
No.of branches	4.4	.57 (13)	3.9- 5.2	1.22	7
Cone angle	32.9°	18.84 (57)	3.1-64.8	2.68**	36
Cone serotiny	0.546	.344(63)	.083-1.00	1.82**	21
Cone abundance	12.58	8.24 (66)	1.3-29.2	2.51**	34

[1] Numbers in parentheses are percent of the plantation mean

[2] ** indicates significant at 1 percent level

[3] Proportion = $\frac{\sigma_G^2}{\sigma_G^2 + \sigma_E^2}$

As latitude increases, tree growth rate decreases. Also, diameter and crown width decrease as both latitude and longitude increase and are smallest in the northwestern part of the species range.

The D^2 values from the Mahalanobis distance function generated by the computer were used to group the 90 seed sources into clusters.

Table 2.--Simple correlation coefficients (r) for 9 traits and 3 geographic gradients

	1 Height	2 Diameter	3 Bark thickness	4 Crown width	5 Branch angle	6 No. of branches	7 Cone angle	8 Cone serotiny	9 Cone abundance	10 Latitude	11 Longitude	12 Elevation
1. Height	1.0				1/							
2. Diameter	.887**2/	1.0										
3. Bark thickness	.703**	.806**	1.0									
4. Crown width	.783**	.839**	.673**	1.0								
5. Branch angle	-.038	-.062	-.138	.064	1.0							
6. No. of branches	.360**	.337**	.146**	.261**	.099*	1.0						
7. Cone angle	-.091*	-.049	.095*	-.064	-.069	.032	1.0					
8. Cone serotiny	.025	-.010	-.030	.002	-.053	.009	-.028	1.0				
9. Cone abundance	.297**	.305**	.090*	.353**	.091*	.198**	-.253**	-.101*	1.0			
10. Latitude	-.393**	-.409**	-.453**	-.453**	.065	-.063	-.147**	.076	-.096*	1.0		
11. Longitude	-.073	-.151**	-.037	-.220**	-.125**	-.090*	-.138**	.124**	-.134**	--	1.0	
12. Elevation	.013	-.025	.009	-.067	.009	-.051	-.077	.042	-.021	--	--	1.0

1/ Coefficients in the block are based on data of 5 replications and others are based on 3 replications.

2/ Significant at 1 percent level (**) or 5 percent level (*).

Then, I plotted a dendrograph on the computed within- and between-cluster distances. On the dendrograph, degree of similarity was expressed by the distance between clusters--the shorter the distance between clusters, the more similar they were to each other.

Examination of distances between seed sources and distances within prospective clusters led to the decision to divide seed sources into five final clusters. Cluster A contains 30 seed sources mostly from Ontario, southern Quebec, and eastern Manitoba (table 3 and fig. 2). In cluster B there are 17 seed sources mostly from eastern Quebec, southern Ontario, and along the St. Lawrence River plus several from Alberta, Manitoba, and western Ontario. Three seed sources from the Northwest Territories and Alberta in the western portion of the natural distribution of jack pine plus one source from northwestern Quebec make up cluster C. Cluster D contains 25 seed sources mainly from the eastern portion of the species range (southern Ontario, southeastern Quebec, northern New York, New Hampshire, Maine and Nova Scotia. The last and most distinct cluster, E, is made up of sources primarily from the Lake States. They are taller, have broader crowns, more accute branch angles, larger cone angles, higher serotiny frequency, and fewer cones compared to plantation averages.

Table 3.--Seed sources after grouped into clusters

Clusters	No. of seed sources	Seed sources
A	30	51, 63, 48, 33, 83, 47, 49, 60, 26, 76, 89, 64, 50, 57, 44, 82, 86, 58, 46, 40, 8, 42, 84, 10, 87, 55, 90, 91, 85, 81
B	17	31, 41, 16, 39, 88, 30, 32, 62, 15, 18, 4, 13, 95, 77, 92, 94, 20
C	4	53, 97, 93, 99
D	25	27, 35, 98, 12, 38, 19, 25, 36, 5, 28, 34, 29, 11, 70, 6, 9, 56, 7, 23, 21, 61, 22, 24, 37, 14
E	14	68, 72, 69, 66, 65, 78, 67, 80, 73, 79, 71, 74, 75, 54

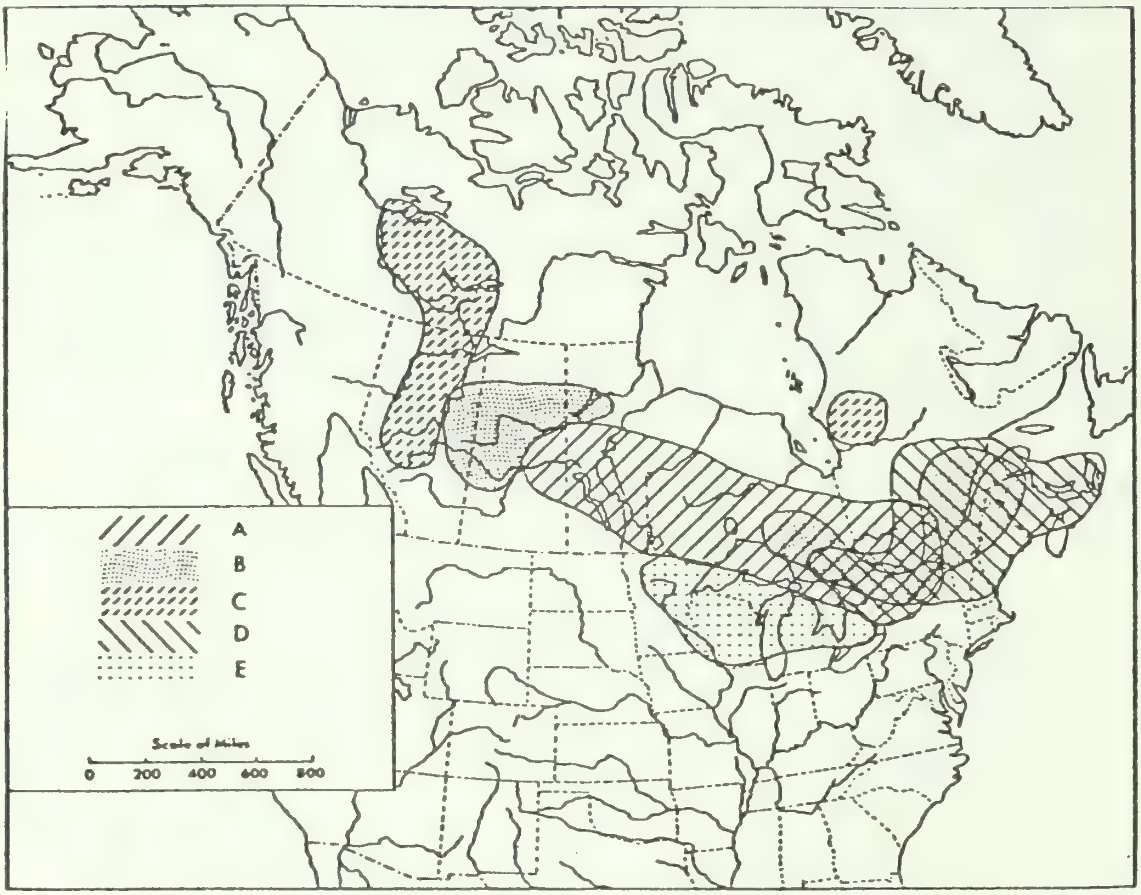

Fig. 2. Proposed subpopulations derived from the dendrograph of the cluster analysis.

Clusters C and E are geographically the most distinct but cluster A is also fairly clear (fig. 2). Clusters B and D do not occupy clearly separated geographic regions.

These results were compared with the results of the study of geographic variation in jack pine done in natural stands by Schoenike (1976). Cluster E, the Lake States group, covers an area similar to that occupied by two of his groups. However, clusters A, B, C, and D are different from any of Schoenike's groups. This is not unexpected because different materials were used for the two studies, the data were collected in different ways, and different traits were evaluated. However, both studies suggest somewhat similar geographic grouping that can be used in working with the species.

CONCLUSIONS

1. There are large variations among seed sources in the 10 traits measured.

2. Most traits that are related to tree growth show large differences in seed source location.

3. Latitude of seed source affected height, diameter, bark thickness, and crown width.

4. Cluster analysis provided a strong indication of geographically defined populations that can be used for tree and seed source improvement.

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INTRASPECIFIC VARIATION IN HIMALAYAN WHITE PINE, PINUS GRIFFITHII [1]

John B. Genys[2]

ABSTRACT.--Twenty-one seed sources of Himalayan white pine (Pinus griffithii McClel.) (11 from native stands and 10 from planted trees) were studied in Maryland's State Forest Tree Nursery and in 11 plantations in Maine, Maryland, Michigan, Illinois and North Carolina. In the nursery, intraspecific variations were observed in leaf lengths, time of bud-set, tendency for secondary growth, and 2-year heights and diameters. Survival rates in Maryland's Piedmont Plateau and coastal plain, and in North Carolina were satisfactory. In Maine, New York, Michigan, Illinois and Maryland's Allegheny Mountains, P. griffithii either completely failed or showed very poor survival. Some strains from Pakistan were more winter-hardy than those from India or Bhutan. In two Maryland plantations best growth rates were attained by populations from Uttar Pradish in India, Shorgan in Pakistan, and from three locations of planted trees. In New York and North Carolina plantations, Himalayan white pine was attacked by white pine weevil (Pissodes strobi Peck).

Himalayan white pine (Pinus griffithii McClelland) was named and described in 1854. Some synonyms are P. excelsa Wallich ex. D. Don, P. wallichiana A. B. Jackson, and P. nepalensis De Chambey. In India, common names are blue pine, kail or biar. Some writers have called it Bhutan pine, Bohtan pine, Nepal pine, or because of white granules on its leaves -- "pine of tears" (Tränenkiefer).

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Morphologically, Himalayan white pine is a close relative to other white pines of subsection Strobi (Konar 1960). In comparison to eastern white pine (P. strobus L.), this species has longer, drooping, more bluish green leaves, larger cones (15 to 30 cm long), and larger seeds. In its native range, it reaches heights of 100 to over 160 feet. P. griffithii includes several known horticultural forms: P.g. form monophylla Carr. (needles in a single bundle), P.g. form zebrina Croux (needles golden-yellowish with white cross-stripes), and P. g. form nana R. Smith (dwarf-like). However, there are no described botanical varieties.

The natural range of Himalayan white pine extends along the southern slopes of the western and central Himalayan Mountains from eastern Afghanistan, through northern West Pakistan, southern Kashmir, Jammu and Punjab provinces of India, Nepal, Sikkim and Bhutan, to isolated populations in Assam, eastern Tibet and northern Burma. It is most common at elevations from 6,000 to 10,000 feet, but occurs as low as 4,000 feet and as high as 12,500 feet. Within this range, P. griffithii is the only pine of subsection Strobi; therefore, it does not cross naturally with other pines in its native habitats. It has been crossed artifically with other white pines, and the hybrid of P. griffithii x P. strobus grows rapidly (Meyer 1954).

Himalayan white pine has been planted in all continents outside its range. In the United States, individual specimens are found in all northeastern states, but they are most common in the area near Philadelphia, Pennsylvania (Wright 1958). In comparison to P. strobus, the growth of Himalayan white pine is faster at Rochester, N.Y., but slower at the Pack Forest in New York.

A report by Lemmien and Wright (1963) indicates that Himalayan white pine can grow as far north as southern Michigan. A few 32-year-old trees were 52 feet tall and had 12-inch diameters breast high. In comparison to P. strobus, they had smaller heights, but slightly larger diameters.

In Maryland, the author has registered small plantings of P. griffithii at about 20 locations. The three largest Himalayan white pines in the U.S.A. grow near Catonsville, Maryland. At age 38 they were about 75 feet tall, had straight stems, and were healthy in all respects. Natural reproduction at this location indicate that Himalayan white pine is able to reproduce when planted outside its natural range.

Wright and Gabriel (1959) reported that some trees were injured and killed in Philadelphia during a severe winter of 1933-34; at the George Landis Arboretum in New York, it is classified as "not successful" because young seedlings are killed by early frost (personal communication with Fred Lape, Director); while in Highland Park of

Rochester, New York, two specimens of Himalayan white pine grew very well. Himalayan pine suffers from attacks by the white pine weevil (Pissodes strobi Peck) in southern Connecticut (Bailey 1955), and Genys (1977) reported from Maryland that P. griffithii can be attacked by Nantucket pine tip moth (Rhyacionia frustrana Comstock). One of the best traits of this species is its high degree of resistance to white pine blister rust (Cronartium ribicola Fischer) (Heimburger 1956, Wright and Gabriel 1959).

In the present study, Himalayan white pine was represented by 11 seed sources from native stands and 10 from trees planted in the United States and Italy. The major objectives were:

(1) To determine the nature and extend of genetic variation in Himalayan white pine, and

(2) to determine the potential for selection of frost-hardy Himalayan white pine for planting in northern regions of the eastern United States.

MATERIALS AND METHODS OF STUDY

Twenty-one seedlots for this experiment were acquired in 1961 and 1962 from 11 native stands in Pakistan, India and Bhutan, and 10 trees planted in the United States and Italy. A random sample of 50 filled seeds from each lot was used for determination of 1000-seed weights (data code No. 6 in table 1).

Two experiments were conducted at the State Forest Tree Nursery in Harmans, Maryland (latitude 39°07'N, longitude 76°45'W). This site is in plant hardiness zone 7 with average annual minimum temperatures ranging from 0° to 10°F, a frost-free period lasting from 180 to 210 days, and the first fall frost occurring between October 30th and November 10th.

The first experiment in the nursery was started on November 19, 1962. Twenty seed lots were used to establish a 4-times replicated, randomized block experiment using 2-foot rows as plots. Seedlings were spaced 2 inches apart within rows and 6 inches between rows. Bulk plots of seedlings were also grown for field plantings. The replicated plots were used for studies of coded characteristics as follows:

(8) Needle length

(9) The day of the year when 50 percent of 1-year-old seedlings set terminal buds,

(11) The percent of 1-year-old trees exhibiting secondary growth (resuming growth after terminal buds were once formed),

(12) The 2-year height based on the plot averages of the four largest seedlings representing four quarters of row-plots, and,

(13) The 2-year diameter above groundline on the three largest sample trees, dug from each plot before planting.

A second similar experiment in the nursery was established in spring 1967, using seed-lots of 15 sources. This time, two characteristics were studied:

(10) The percent of 2-year-old trees with terminal buds on October 24, 1968, and,

(14) The 2-year heights.

During the springs 1965, 1966 and 1967, the trees seeded in November 1962 were planted in Maryland (on 3 sites), Michigan (on 3 sites), Illinois (on 2 sites), Maine (1), New York (1), and North Carolina (1). Site descriptions, the age of stock and experimental designs of these plantations are given in the accompanying list.

Survival and heights were studied at various ages. Data in this report were based on 10- and 12-year-old trees. Heights are included for the two plantations in Maryland which had sufficient numbers of trees. White pine weevil (Pissodes strobi) was studied in the New York and North Carolina plantations.

Analysis of variance was based on the randomized block design. The least significant differences (L.S.D.) were determined by the Duncan's multiple range test. Character correlation and the correlations between measured characteristics and geographic data were also determined; only significant correlations will be discussed in the text.

RESULTS

Characteristics of Seedlings in the Nursery

Seed weights

Weights of 1000 filled seeds of P. griffithii from 9 stands and 10 individual tree collections varied from 36 grams (collected from a planted tree in Catonsville, Md.) to 77 grams (collected in Oxford, Md.). There was less variation among the seed lots from the native stands (table 1). For the stand collections, the correlation between the seed weights and eastern longitude was $r = .-73^*$ (d.f. = 6). Seeds from West Pakistan tended to be heavier than those from India and Bhutan.

List of research sites, experimental design, dates of planting, and age of stock

Maryland, Carroll Co., Piedmont Plateau, near Liberty Lake; 39°23'n; 76°54'W; elev. 490 ft; property of City of Baltimore; a former farm field; fertile, good drainage.	March, 1965; 2-0 stock; 4-tree square plots; spacing 7 ft x 7 ft; 21 populations; replicated in 4 blocks; measured at age 10.
Maryland, Anne Arundel Co., coastal plain, near Annapolis; 39°02'N; 76°24'W; elev. 15 ft; property of State of Md.; poor drainage; fertile soil.	April, 1965; 2-0 stock; 4-tree square plots; spacing 7 ft x 7 ft; 21 populations, replicated in 4 blocks; measured at age 10.
Maryland, Garrett Co., mid-Appalachian Mtns., Pleasant Valley Research Center; 39°3'N, 79°14'W; elev. 2600 ft; rocky and shallow soil; growing season about 130 days, cold winters.	April, 1965; 2-0 stock, spaced at 7 ft x 7 ft; 4-tree plots; 21 populations; replicated in 4 blocks. Last measurements made in Fall 1974.
Michigan, Kalamazoo Co., Kellogg Farm, near Hickory Corners; elev. 700 ft, slopes 3 to 30%; brush killed by 2,4,5-T; soil sandy loam to loamy sand.	April 9, 1966; 2-1 stock; spaced 8 ft x 6 ft; 4-tree row plot, 11 strains, replicated in 4 blocks. Last measurements made on July 17, 1974.
Michigan, Cass Co., Fred Russ Forest; elev. 700 ft; previous corn field, moved, and 3-foot strips sprayed with aminotriazole.	March 3, 1966; 2-1 stock; 4-tree plots; 10 strains replicated in 4 blocks. Last measurements on July 17, 1974.
Michigan, Ingham Co., Tree Research Center; elev. 700 ft; moist site, moderately well drained silt soil.	April 9, 1966; 2-1 stock; spaced 8 ft x 6 ft; 4-tree row plots; 12 populations; 2 blocks. Last measurements: early summer 1974.
Maine, Penobscot Co., near Olamon; state-owned land; 45°8'N, 68°35'W; elev. 200 ft; moderately well drained, 2 ft deep, sandy loam soil.	May 1967; 2-2 stock; originally 16 populations; 8 blocks; only 4 blocks were complete.

List of research sites, experimental design, dates of planting, and age of stock. cont.

New York, Warren Co., Heiberg Memorial Forest, north of Warrensburg.	April 1965; 2-0 stock; 15 populations; 4-tree square plots in 4 blocks.
Illinois, Henderson Co., Oquawka; level, loamy sand soil, dry in summer.	April 16, 1965; 2-0 stock; 6 populations in 4 blocks, represented by 4-tree plots; trees spaced at 7 ft x 7 ft. in 1974 only 3 blocks available for analysis.
Illinois, Edwards Co., West Salem; level, silty loam site. Simazine was applied after planting.	April 16, 1965; 2-0 stock; 6 populations in 5 blocks represented by 4-tree plots; trees spaced at 7 ft x 7 ft.
North Carolina, Madison Co., near Mars Hill, north of Asheville, southern slopes of south Appalachian Mtns.; shallow, rocky soil.	April, 1965; 2-0 stock; 15 populations, replicated in 4 blocks; 4-tree square plots; spacing 6 ft x 8 ft; some trees were currently injured by fire when measured in Spring 1975.

Leaf lengths

Leaf lengths in 6 of the provenance collections and 6 families ranged from 8.9 cm (No. 589 from a tree planted in Oxford, Md.) to 12.3 cm (No. 282 from Pakistan). Five out of six populations from the native range had longer needles than those from the planted trees.

Setting of terminal buds

Setting of terminal buds in the fall was studied twice in the nursery. Twelve populations (6 representing provenances and 6 single tree families) studied in fall 1964 set their terminal buds during the period from October 23 to November 7. Populations with the latest budset originated from planted trees (Nos. 589, 588, and 596). Populations from native stands showed only a 5-day variation in bud set date. Date of bud set was negatively correlated with the leaf length ($r = -.72^{**}$ d.f. = 10) suggesting that populations with short leaves set their buds earlier.

On October 24, 1968, twelve populations (10 representing provenances and 2 single tree families) of 2-year-old trees had different numbers of trees with terminal buds, ranging from only 2 percent (No. 721 from Bhutan) to 32 percent (No. 762 from Rochester, N. Y.). These two populations, showing extreme values in bud set, also showed extreme values in their survival rates in cold regions. All trees of population No. 721 set buds late and all died; trees from Rochester set their buds early and showed the best survival. The percent of trees with buds was negatively correlated with eastern longitude ($r = -.85^{**}$ d.f. = 7).

Secondary growth

In the six provenances and 6 families studied, the tendency for secondary growth (starting growth after primary terminal bud was formed) varied significantly (table 1). Some populations had as few as 23 percent of trees with secondary growth (No. 282 from Pakistan), while others had 74 percent (No. 592 from Annapolis, Md.). This characteristic showed no significant correlation to geographic data, and, contrary to expectation, it was not related to the survival rates in the northern regions.

Two-year height growth

In 1964 the 2-year-old Himalayan white pines (9 provenances, 6 families) averaged 12.2 cm in height. Variation among populations ranged from 84 percent (Nos. 588 and 596 from planted trees in Maryland) to 119 percent (No. 589 from trees planted in Maryland) of the mean for all populations. In 1968 (10 provenances, 2 families), 2-year heights averaged 8.5 cm, and differences among populations

Table 1.--Origin and growth data of different populations of Himalayan white pine (Pinus griffithii) studied in Maryland (at the State Forest Tree Nursery) in 1963-64, and 1967-68 (2-year heights)

Code:	(2)	(3)	(4)	(6)	(8)	(9)	(10)	(11)	(12)	(13)	(14)
Seed	Seed origin-country			1000		Bud set		Trees	Two-year data		
lot	Longi-	Lati-	Alti-	seed	Needle	Day of	10/24	w/2nd	1964		1968
no.	tude	tude	tude	weight	length	year	trees	growth	Height	Diam.	Height
Mean height or diameter in cm:									12.2	.42	8.5
			Feet	Grams	Cm		Percent	Percent	---- Percent of mean----		
Pakistan											
719	67°30'	29°00'	7500	65	--	--	26	--	107	--	107
756	72°22'	34°04'	7500	--	--	--	--	--	--	--	--
720	73°12'	33°30'	7000	51	--	--	13	--	92	--	100
103	73°15'	35°38'	6500	53	11.6	302	17	37	99	98	104
282	73°20'	34°10'	7900	56	12.3	304	9	23	111	95	102
280	73°20'	34°10'	7600	59	11.2	302	14	51	117	117	107
281	73°30'	34°	7500	66	11.6	303	12	54	110	110	119
India											
296	77°14'	32°15'	6200	51	10.5	304	10	35	102	100	95
771	78°	31°	7200	--	--	--	5	--	102	--	123
297	--	--	7000	46	11.7	307	17	65	111	107	110
Bhutan											
721	86°06'	27°42'	7500	46	--	--	2	--	--	--	94
Planted trees											
106	Italy			55	10.2	307	--	37	102	100	--
586	Catonsville, Md. (No. 1)			62	--	--	--	--	--	--	--
587	Catonsville, Md. (No. 2)			63	10.8	305	--	36	88	--	--
588	Catonsville, Md. (No. 3)			36	10.8	308	--	39	84	86	--
589	Oxford, Md. (No. 1)			77	8.9	311	--	45	119	102	--
592	Annapolis, Md. (No. 2)			71	10.0	306	--	74	101	95	--
596	Solomons, Md.			58	9.6	308	6	38	84	88	80
598	Washington, D.C. (No. 1)			74	--	--	--	--	--	--	--
641	Easton, Md.			72	--	--	--	--	--	--	--
762	Rochester, NY			49	--	--	32	--	--	--	83
The least significant difference at 0.05 level				--	2.7	ns	16	38	30	27	19

varied from 80 percent (No. 596 from Solomons, Md.) to 123 percent (No. 771 from India) of the mean. Two-year heights of the same populations, studied in 1964 and 1968, showed a significant positive correlation ($r = .63^{*}$ d.f. = 8).

In 1964 (6 provenances, 5 families), basal diameters averaged 0.42 cm and differences among populations ranged from 86 percent (No. 588 from Catonsville, Md.) to 117 percent (No. 280 from Pakistan). Diameters were significantly correlated with the 2-year heights measured in 1964 and 1968 ($r = .81^{**}$ d.f. = 9 and $.78^{*}$ d.f. = 5, respectively).

Characteristics after Planting

Data on survival in three plantations, heights in two plantations, and white pine weevil attack in two plantations are summarized in table 2.

Survival

Survival rates of Himalayan white pine varied in different climatic regions, and were related to the origin of seed source.

Survival in Maine, New York, Michigan, Illinois and Garrett County, Maryland, of Himalayan white pine was very poor at all sites located in plant-hardiness zones 3, 4 and 5, where the average annual minimum temperatures are -5°F or lower. In all this region, more than half of the populations had 0 percent survival, and none of the populations had more than 31 percent of trees living. Among the provenances showing best survival (13 percent) were Nos. 280, 282 and 719 from West Pakistan. Of the single tree families, Nos. 106, 586 and 762 were among the best. Trees from higher elevations showed somewhat better survival than those from lower elevations. In the Garrett County, Md. plantation, trees with early budset tended to have higher survival rates.

In Maryland plantations located in the Piedmont Plateau (Carroll County) and Atlantic Coastal Plain (Anne Arundel County) within plant hardiness zone 6, Himalayan white pine survived as well as eastern white pine. In Carroll County, survival rates among the 11 provenance collections and 10 families ranged from 0 percent (No. 721 from Bhutan) to 100 percent (No. 592 from Annapolis, Md.) and about two-thirds of the populations had survival rates exceeding 50 percent). Survival rates in this plantation were positively correlated with survival rates in the Anne Arundel County, Md. ($r = .72^{**}$d.f. = 19) plantation, and negatively correlated with longitude ($r = -.69^{*}$ d.f. = 9). In Anne Arundel County, survival rates among populations ranged from 13 percent (No. 721 from Bhutan) to 100 percent (No. 587 from Catonsville, Md.), and 19 of 21 populations had survival rates greater than 50 percent. In this plantation, survival rates were also negatively correlated with longitude of seed source ($r = -.85^{**}$ d.f.-9) (table 2).

Table 2.--Survival and growth rates of different populations of Himalayan white pine, Pinus griffithii, in eastern United States (some data on attack by white pine weevil, Pissodes strobi, are also included)

Code	(2)	(3)	(4)	(20)	(21)	(22)	(23)	(24)	(26)	(27)
Seed	Seed origin-country			Survival			Height		Weevil attack*	
lot no.	Longitude	Latitude	Altitude	Carroll County Md.	Anne Arun. County Md.	North Carolina	Carroll County Md.	Anne Arun. County Md.	New York	North Carolina
Age of studied trees (yrs)				10	10	12	10	10	-	-
Mean height x̄ (feet):				-	-	-	5.8	5.1	-	-
			Feet	----------Percent----------------			Percent of mean		Number	
Pakistan										
719	67°30'	29°00'	7500	50	81	25	115	114	0/1	1/4
756	72°22'	34°04'	7500	94	88	--	89	103	--	--
720	73°12'	33°12'	7000	44	81	--	--	77	--	--
103	73°15'	35°38'	6500	63	63	19	89	91	--	3/3
282	73°20'	34°10'	7900	38	67	6	--	112	0/2	0/1
280	73°20'	34°10'	7600	75	75	31	124	97	0/2	2/5
281	73°30'	34°	7500	63	88	31	104	105	0/1	3/3
India										
296	77°14'	32°15'	6200	44	44	6	--	--	--	1/1
771	78°	31°	7200	56	75	6	123	138	--	1/1
297	--	--	7000	44	56	19	82	105	0/1	3/3
Bhutan										
721	89°06'	27°42'	7500	0	13	0	--	--	--	--
Planted trees										
106	Italy			56	67	25	91	125	1/3	3/4
586	Catonsville, Md.(No. 1)			67	94	--	70	97	1/3	--
587	Catonsville, Md.(No. 2)			88	100	13	107	108	--	1/3
588	Catonsville, Md.(No. 3)			67	75	13	--	84	--	0/2
589	Oxford, Md. (No. 1)			50	81	25	--	77	--	2/4
592	Annapolis, Md. (No. 2)			100	75	31	84	76	--	2/5
596	Solomons, Md.			63	88	0	--	94	0/1	--
598	Washington, D.C.(No. 1)			56	81	--	130	119	--	--
641	Easton, Md.			44	75	--	130	138	--	--
762	Rochester, N.Y.			75	88	--	91	68	0/3	--
The least significant difference at 0.05 level				68	56	ns	70	61	--	--

* trees attacked by Pissodes strobi (left): trees studied (right).

The North Carolina plantation is located in the transition region of plant hardiness zones 6 and 7. On this site, Himalayan white pine (9 provenances, 6 families) showed a better survival than in the northern regions, but worse than in Maryland's hardiness zone 6. Survival rates ranged from 0 percent (Nos. 721 from Bhutan, and 596 from Solomons, Md.) to 31 percent (Nos. 280 and 281 from Pakistan and No. 592 from Annapolis, Md.). Survival in North Carolina was correlated with survival in Carroll County, Md. ($r = 0.52^*$ d.f. = 13) and was correlated with diameters of 2-year-old trees ($r = .64^*$ d.f. = 9).

Height growth in plantations

Heights are only reported for the two plantations in Maryland (Carroll and Anne Arundel Counties) with good survival.

In Carroll County, heights of 10-year-old trees averaged 5.8 feet. Heights of different populations and families ranged from 70 percent to 130 percent of the plantation mean. The slowest growing family was from planted tree No. 1 in Catonsville, Maryland (No. 586). The fastest growing families originated from planted trees in Washington, D.C. (No. 598) and Easton, Md. (No. 641), followed by populations from Pakistan (No. 280) and India (No. 771). Heights in this plantation were significantly correlated with diameters of 2-year-old trees ($r = .82^*$ d.f. = 4) and with heights of 10-year-old trees in Anne Arundel County, Md. ($r = .60^*$ d.f. = 12).

In Anne Arundel County, 10-year-old trees had an average height of 5.1 feet. Heights of different populations and families ranged from 68 percent to 138 percent of the plantation mean. Slowest growing were the families from Rochester, N.Y. (No. 762), Annapolis, Md. (No. 592), Oxford, Md. (No. 589), and the population from Pakistan (No.720). The fastest growing were again the family from Easton, Md. (No. 641), and the populations from India (No. 771), and Italy (No. 106). Heights in this plantation were significantly correlated with latitude ($r = .75^*$ d.f. = 6).

In summary, the best families were from planted trees No. 641 in Easton, Maryland, and No. 598 in Washington, D.C., and from native stands No. 771 in Pradish, India, and No. 719 in Shogran, West Pakistan. With the exception of the populations No. 280 from West Pakistan and family No. 106 from Italy, rankings were rather similar at the two sites.

Reliability of early growth data

If trees were selected for rapid growth on the basis of 2-year heights in 1964, populations No. 589, 280, 282 and 297 would be included. However, none of these populations were among the four best at age 10. In fact, 2-year heights of the first experiment

(1963-1964) showed no relationship to 10-year heights in the Maryland plantations (r = .20 and .14). Much more reliable for prediction of 10-year heights were the 2-year diameters ($r = .82^{*}$ d.f. = 4 and r = .26 d.f. = 8) and 2-year heights of seedlings studied in 1967-1968 (r - .57 d.f. = 5, and r = .45 d.f. = 8).

Attack by white pine weevil

White pine weevil (*Pissodes strobi*) was studied in New York and North Carolina (table 2). In New York, out of 17 surviving trees, two (12 percent) were attacked by white pine weevil. In North Carolina, weevil attack was more extensive, and out of 39 trees, 22 (56 percent) were injured. In this plantation, populations from low elevations (like No. 103) included more trees attacked by white pine weevil than those from higher elevations (like No. 282), and the correlation of the numbers of attacked trees with the elevation of the seed-source was $r = -.84^{**}$ d.f. = 6

Cone production

In North Carolina, at age 12, about 10 percent of Himalayan white pine had cones. The most pronounced cone producer was population No. 280 from Pakistan. Out of 4 trees studied, 3 had cones. In general, at this early age, *P. griffithii* had fewer cones than *P. strobus* (20 percent of trees with cones).

Comparison of Himalayan White Pine with Eastern White Pine

In comparison to *P. strobus*, Himalayan white pine had heavier seeds, and when growing on the same sites longer leaves, smaller 2-year heights, larger 2-year diameters, more trees with secondary growth, and set terminal buds later in the fall. When planted in the field and studied for 8 or 10 years, Himalayan white pine had significantly greater mortality than *P. strobus* in Maine, New York, Michigan, Illinois, Garrett County, Md., and North Carolina. It survived nearly as well as *P. strobus* in Carroll County, Md., and showed a similar survival rate in Anne Arundel County. In Maryland's Piedmont Plateau and Coastal Plain, Himalayan white pine had smaller 10-year heights than eastern white pine. In North Carolina, both species had similar percentages of trees attacked by *Pissodes strobi*, Himalayan white pine had fewer trees with cones. While the characteristics listed above were distinctly different, in other measurements one species were within the range of the other species. Such overlapping ranges at variation were in numbers of cotyledons, time of bud-set, and growth rates of different populations.

DISCUSSION

Results on seed weight, date of bud-set, percent of trees with secondary growth, and growth rate of 2-year-old trees are mainly of basic interest, while the survival rates of different populations planted in the northern regions of eastern United States are of more practical importance. Also important are the data on variation in growth rates of 10-year-old trees.

Studies on survival rates in various hardiness zones lead to identification of several general trends. In the northern plantations, except in Illinois, populations Nos. 280, 281 and 719 from Pakistan were most promising. In all plantations, population No. 721 from Bhutan failed completely, and population No. 762 from a planted tree in Rochester, N.Y. showed the best or the second best survival. Correlation analysis suggests that survival rates were negatively correlated with the eastern longitude and the date of bud-set, and positively correlated with the elevation of seed source. Apparently, best survival rates can be expected from the seed sources from western longitudes, higher altitudes, and populations setting terminal buds early in the fall. Also, good survival can be expected from some progenies originating from planted trees in northern regions (like Rochester, New York).

Contrary to many instances in other pines, the growth rates of P. griffithii showed a positive relationship with northern latitude and elevation of the seed source. Also, heights showed positive relationships with needle lengths and diameters of 2-year-old seedlings, and a negative correlation with day of budset and the percent of trees with secondary growth.

If selection of seed sources for rapid growth are based on these current results, most likely trees planted in Easton, Maryland (No. 641) and Washington, D.C. (No. 598), would be recommended for use as seed sources. Among the populations from the native region, most promising were No. 771 from India for warmer regions and Nos. 719, 282 and 280 from Pakistan for colder regions.

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THE BIONOMICS OF THE COTTONWOOD LEAF BEETLE, CHRYSOMELA SCRIPTA FAB., ON TISSUE CULTURE HYBRID POPLARS[1]

T. R. Burkot and D. M. Benjamin[2]

ABSTRACT.--Tissue culture methods are applied to poplars of the Aigeiros group in attempts to overcome premature decline thought to be associated with viral infections. Hybrid selections from such cultures outplanted in 1975 at the F. G. Wilson Nursery in Boscobel, Wisconsin subsequently were severely infested by the Cottonwood Leaf Beetle, Chrysomela scripta Fab. Beetle populations built up rapidly in spring 1977 and severe defoliation occurred; an average of 45% of the terminal buds were destroyed and 73 percent of the tips of a preferred clone were fed upon. Younger foliage appeared preferred and certain clones sustained more feeding in field and laboratory studies. Plants receiving greater amounts of overhead irrigation were least defoliated. Rapid increases in the numbers of the insect in Wisconsin are reflected in the following facts. The Cottonwood Leaf Beetle has a rapid life cycle (19 days at 27°C). Consequently, the insect undergoes 4-5 generations per year in Wisconsin where it exhibits a high fecundity of approximately 510 eggs. Finally, because of the larval defensive secretion, salicylaldehyde, the insect has few natural enemies; mainly predatory pentatomids on larvae and adults, and Shizonotus latus Walker, a pupal parasite.

Black poplars of the Aigeiros group maintained by the University of Wisconsin were undergoing premature decline, thought to be associated with viral infections. In an attempt to culture poplars for high yields, heat treatment followed by tissue culture methods were applied to the apical meristems to eliminate viruses. Heat treatments allow the trees to outgrow viruses and shoot-tip culture capitalizes on the absence or

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lowered concentration of viral particles in the apical meristems (Hollings 1965). Such clonal propagation might allow genetically superior traits to be transferred by eliminating the chance of gene recombination occurring via a sexual cycle. However, a wide range of variation for height, number of branches, and leaf traits were discovered among subclones. The basis of this variation is as yet unknown, but the more obvious possible causes include incomplete elimination of viral infection, gene mutation, and chromosomal instability (Lester and Berbee 1977).

Hybrid selections of these subclones were outplanted in 1975 at the F. G. Wilson Nursery at Boscobel, Wisconsin, and subsequently were severely infested by the Cottonwood Leaf Beetle, Chrysomela scripta Fab. The defoliator, although it rarely reaches epidemic numbers in natural stands of Populus, Alnus, and Salix, has become an established annual problem in the monoculture cottonwood plantations of the South, as well as in the nurseries of Wisconsin.

In Mississippi, the insect increased rapidly in numbers because of its high natural fecundity of 823 eggs, a short life cycle, and as many as seven generations per year (Head and Neel 1973). In addition, the Cottonwood Leaf Beetle has few natural enemies because of its defensive secretation, salicylaldehyde, which is exuded by eversible glands on the thorax and abdomen (Wallace and Blum 1969).

We are studying the bionomics of the Cottonwood Leaf Beetle in Wisconsin to develop means of preventing the insects from reaching numbers that result in severe defoliation and destruction of apical tips. In addition, since the tissue cultured hybrid poplar subclones showed variability in vigor and other characteristics, we expect that there would be variability in resistance to insect attack. We will try to develop a method of screening clones for relative resistance.

METHODS

In May, 1977, three Latin squares were established at the F. G. Wilson Nursery at Boscobel, Wisconsin: each square consisted of 25 trees, five trees from each of four of tissue culture Aigeiros subclones and five trees from a tissue culture Lombardy clone. The three Latin squares made up one replicate. A second replicate of these three Latin squares was planted at the University Experimental Farms in Arlington, Wisconsin, in May, 1977. Twice weekly, a count was made of all eggs, larvae, pupae, and adults of the Cottonwood Leaf Beetle on each of the trees in the three Latin squares at the Arlington and Boscobel sites. In addition, a field plot of 1512 tissue culture poplars consisting of six subclones planted in 1975 at the F. G. Wilson Nursery at Boscobel, Wisconsin, served as a third site for biological observations of the Cottonwood Leaf Beetle. Eggs, larvae and pupae were also collected from this field plot and reared in the laboratory for parasites. A record was made of predators seen on the trees. These data later will be incorporated into life tables.

At the end of each generation of the Cottonwood Leaf Beetle, a count was made of all the host apical tips destroyed in the plots to evaluate the economic damage and relative change in insect numbers.

Leaves on which eggs were laid were transferred to environmental chambers at different temperatures (10°C, 17°C, 21°C, 23°C, 27°C, 28°C) to determine the effects of temperature on developmental times and mortality; all rearing occurred at an 18-hour photoperiod.

Virgin males and females were paired and caged in 21.5 cm x 6.7 cm x 5.8 cm plastic boxes with foliage and placed in an environmental chamber at 27°C and 18 hrs of light. Daily counts were made of eggs laid to determine the average fecundity.

The number of larval instars was determined by measuring the head capsule widths of ten larvae daily throughout their development.

Adult preferential feeding tests were carried out by offering a caged male and female a choice of one leaf from each of two different subclones. Leaves of the approximate same size and relative position on their respective trees were used in each replicate. The turgor of the leaves was maintained by keeping the petioles of the leaves submerged in a vial of water plugged at the top with cotton. The tests were run for a week at 27°C, 18 hrs light. The area of the leaves was determined before and after feeding by using a plane polarimeter. The relative feeding preference by adult beetles on mature versus immature foliage from the same clone were likewise tested.

RESULTS

In Wisconsin, the Cottonwood Leaf Beetle has 4-5 generations per year. In the laboratory the females exhibit an average fecundity of 510 ± 153 eggs. The insect has three larvel instars and a short life cycle of 19 days at 27°C; optimal development occurred at 23°C.

Field studies showed both the larvae and adults to be defoliators and to prefer to feed on the more tender young leaves near the apical tip. The first and second instars feed by etching the lower surface of the leaves while the third instars and adults may skeletonize the leaves and leave only the main ribs. In addition, the third instars and adults feed on the apical tips and destroy them. Laboratory studies revealed that of the clones tested for adult preferential feeding, only Aigeiros clone 13 showed a significant difference (at α=5% for 2-t-test) from the others; it was preferred by at least four times that of the standard. Immature foliage was likewise preferred by a ratio of 33:1 over mature foliage. In the field plot of 1512 trees, an average of 45 percent of the apical tips were destroyed and 73 percent of Aigeiros clone 13 tips were fed upon.

Natural control agents were unable to maintain the population of the Cottonwood Leaf Beetle on the Boscobel plot in the second generation at a low economic level: Shizonotus latus Walker parasitizes 3.2 percent of the pupae while Coleomagilla maculata DeGreer consumes 12.4 percent of the eggs. The larval predators such as the lacewings, syrphids, and the pentatomids, Podisus maculiventris Say and Perillus bioculatus Fab. were unable to maintain the population of the Cottonwood Leaf Beetle at an acceptable sub-economic damage level. The amount of feeding damage sustained in the Boscobel nursery was inversely related to the amount of water received via an overhead sprinkler system.

On the Arlington replicates; the Cottonwood Leaf Beetle population was too low to evaluate meaningfully except for making biological observations.

DISCUSSION

Several facets of the Cottonwood Leaf Beetle's biology enhance its prospects for being a continuing problem in Populus nurseries in the Lake States. First, is its high fecundity of 510 eggs. Secondly, is its short life cycle which requires 19 days from adult at 27°C. Thirdly, the insect is multivoltine, having 4-5 generations per year in Wisconsin.

A larval defensive secretion repels insect predators and thus appears to restrict the kinds of the biotic control agents that can successfully attack the insect to pentatomids, syrphids and lacewings. Neither the egg predator, Coleomagilla maculata, nor the pupal parasite, Shizonotus latus, can reduce the Cottonwood Leaf Beetle to an economically acceptable level. This enables the beetle to increase rapidly in population. Abiotic factors, notably temperature, seem to mainly control the rapidity of increase. Watering from overhead sprinkler systems also limits the destructiveness of the beetle by knocking the adults off the trees. The more water falling on a plant, the less likely it is that an adult will feed there and oviposit. However, even temperature and overhead watering are unable to prevent the insect from reaching such numbers that an average of 45 percent of the apical tips are destroyed and 73 percent of the tips of the preferred clone are fed upon as at Boscobel.

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HERITABILITY CONSTRUCTION FOR PROVENANCE AND FAMILY SELECTION

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ABSTRACT.--Concepts and procedures for heritability estimations through the variance components and the unified F-statistics approach are described. The variance components approach is illustrated by five possible family selection schemes within a diallel mating test, while the unified F-statistics approach is demonstrated by a geographic variation study. In a balance design, the use of the heritability formula $h^2 = 1-(1/F)$ is recommended. The F value is the same computed F value used in the analysis of variance for testing quality of genetic units.

Heritability is defined as "degree to which a character is influenced by heredity as compared to environment" (Snyder 1972). Although the concept holds in a general sense, heritability estimates vary with the way they are calculated. Heritability can be calculated in four ways: (1) parent-offspring correlation estimates degree of resemblance between parents and offspring; (2) regression estimates the selection differential in offspring as dependent on the selection differential in the parent; (3) intraclass correlation estimates the degree of resemblance among individuals within a genetic classification, and (4) genetic gain divided by selection differential estimates the efficacy of selection. These four methods are interrelated and may be used interchangably, but in certain cases adjustments should be made (Franklin 1974, Squillace 1974).

Heritability and gain estimates apply only to the experiments from which they were obtained. Furthermore, the selection differentials and heritabilities must apply to the same things, which may be individual trees, or family means (Wright 1976). Although single tree heritability and family heritability are formulated in most textbooks (Lerner 1958, Falconer 1960, and Becker 1964), heritability for other genetic units such as stand, ecotype, family within stand, full-sib family within female parent, or family and site combination, are seldom available.

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In this paper we show how to break down phenotypic variation and construct heritabilities according to the experimental design, mating system, and selection scheme that are being used. The purpose is to help persons to make heritability estimates clearer and more consistent. In addition, we propose a unified formula for heritability, $h^2 = 1-(1/F)$, where F is the computed value for testing the null hypothesis that all genetic units are equal. This heritability is useful for predicting genetic gain of the genetic units being tested and selected.

Variance Component Approach

The basic concept of heritability is the genetic variance among units divided by the phenotypic variance among units. Therefore, the procedure for constructing heritability from analysis of variance can be described as follows:

1. Compute phenotypic variance among units
2. Identify variance components
3. Assemble genetic variance
4. Divide genetic variance by phenotypic variance

h^2 in the Clonal Test

In the simplest case, a clonal test, each ramet is assumed to have received total and identical genetic information from the ortet. The phenotypic expression of a seedling is affected by the genetic effect of the ortet and the environmental effect, with the following model:

$$Y_{ij} = \mu + G_i + E_{ij}$$

where Y_{ij} = phenotypic expression of the jth ramet from the ith ortet

μ = population mean in the test

G_i = genetic effect due to the ith ortet (i = 1 to n)

E_{ij} = random independent and normally distributed environmental effect (i = 1 to n, and j = 1 to r)

The ANOVA table is shown in table 1, where Ve and Vg are variance components for environment and genetics, respectively.

Table 1.--Analysis-of-variance table for a completely randomized clonal test

Source	df	MS	EMS
Clone	n-1	$\frac{r}{n-1}\sum_{i=1}^{n}(Y_{i.}-Y_{..})^2$	$Ve + rVg$
Within	n(r-1)	$\frac{1}{n(r-1)}\sum_{i+1}^{n}\sum_{j=1}^{r}(Y_{ij}-Y_{i.})^2$	Ve
Total indiv.	nr-1	$\frac{1}{nr-1}\sum_{i=1}^{n}\sum_{j=1}^{r}(Y_{ij}-Y_{..})^2$	$Ve + \frac{(n-1)r}{nr-1} Vg$

To construct heritability for clonal selection, we proceed as follows:

1. Compute phenotypic variance among clones and record as the value for Clone Mean Square.

2. Identify variance components: obtain Ve + Vg from Expected Mean Square (EMS).

3. Assemble genetic variance; solve two simultaneous equations for Ve and Vg and compute the value for rVg.

4. Divide the value for rVg by the Clone Mean Square.

Clonal heritability obtained is the form of $rVg/(Ve_2 + rVg)$, which is equivalent to the commonly accepted formula: $h^2 = Vg/(Vg + Ve/r)$ (Burton and Devane 1953).

h^2 in a Diallel Mating Test

Following the same procedure, we can construct heritability formulas suitable for various selection schemes after a diallel mating test.

Under the diallel mating scheme, every male mates with every female parent. For monoecious species, diallel mating includes a cross and reciprocal cross with every other tree. The statistical model is a two-way analysis of variance:

$$Y_{ijk} = \mu + M_i + F_j + MF_{ij} + W_{ijk}$$

where Y_{ijk} = the phenotypic value of seedling K produced from the ith male parent and the jth female parent (k = 1 to K).

μ = population mean

M_i = genetic effect from the ith male parent (i = 1 to I)

F_j = genetic effect from the jth female parent (j = 1 to J)

MF_{ij} = interaction between the ith male and jth female parents

W_{ijk} = experimental error (k = 1 to K)

In the conventional diallel analysis, where components are estimated from the ANOVA, heritabilities are estimated for male parents, female parents, and interaction (full-sibs). However, there are other selection schemes possible and each has its own heritability. Computation is possible by considering the sum of squares for the components in the diallel mating scheme.

The partitioning of variance can be facilitated by working with the individual expectation of sum of squares as listed in table 2.

Table 2.--Expectations of sum of square in a completely randomized diallel mating test

Line no.	Item	Interpretation	Coefficient for				
			μ	σ^2_m	σ^2_f	σ^2_{mf}	σ^2_w
1	$\Sigma\Sigma\Sigma X_{ijk}^2$	Individual	IJK	IJK	IJK	IJK	IJK
2	$\Sigma\Sigma X_{ij.}^2/K$	Full-sib	IJK	IJK	IJK	IJK	IJ
3	$\Sigma X_{i..}^2/JK$	Half-sib in male	IJK	IJK	I K	I K	I
4	$\Sigma X_{.j.}^2/IK$	Half-sib in female	IJK	JK	IJK	JK	J
5	$X_{...}^2/IJK$	Correction term	IJK	JK	I K	K	I

Once we obtain the expected variance components for the sum of squares, we can proceed to the intermediate steps in formulating heritability:

A. The sum of squares for a "m" genetic unit within a "n" unit, SSQ m in n, is $SSQ_m - SSQ_n$. For example:

SSQ individual in plantation = SSQ individual - SSQ correction term

SSQ individuals within full-sib = SSQ individual - SSQ full-sib

SSQ full-sib within male parent = SSQ full-sib - SSQ half-sib in male

B. Heritability for differences among "m" units with "n" units is:

$$\frac{\text{Genetic Variance Component in SSQ m in n}}{\text{SSQ m in n}}$$

If we divide both the numerator and the denominator of the above formula by the degrees of freedom associated with the "m in n" unit, the numerator becomes genetic variance (Vg) and the denominator becomes phenotypic variance (Vp), and the result is the commonly accepted formula, $h^2 = Vg/Vp$. It is easier to work with SSQ than MSQ and ignore the degrees of freedom.

If we want to construct heritability for differences among full-sib families within male parent, we first determine the variance components within the SSQ full-sib in male. From lines 2 and 3 of table 2 we have:

$$\begin{aligned}\text{SSQ full-sib in male} &= \text{SSQ full-sib} - \text{SSQ male}\\ &= IK(J-1)\sigma_f^2 + IK(J-1)\sigma_{mf}^2 + I(J-1)\sigma_w^2\end{aligned}$$

If we consider the first two terms as genetic contribution, the numerator in the heritability formula is:

$$IK(J-1)\sigma_f^2 + IK(J-1)\sigma_{mg}^2$$

and the denominator is simply SSQ full-sib in male, or all of its associate variance components.

If we further consider the genetic parameters in terms of additive genetic variance (Va) and dominance variance (Vd), we have $\sigma_f^2 = 1/4\ (Va)$, $\sigma_{mxf}^2 = 1/4\ (Vd)$ and $\sigma_w^2 = 2/4\ (Va) + 3/4\ (Vd) + \sigma_e^2$, and the numerator becomes:

$$IK\ (J-1)1/4(Va) + IK(J-1)1/4(Vd) + I(J-1)\ \{2/4(Va) + 3/4\ (Vd)\}$$

and the denominator becomes:

$$IK(J-1)1/4(Va) + IK(J-1)1/4(Vd) + I(J-1)\ \{2/4(Va) + 3/4(Vd) + Ve\}.$$

While the second consideration is more complete and academic, the first consideration is practical and useful in gain prediction. Heritabilities for family selection are therefore constructed on the basis of the first consideration (table 3).

Table 3.--Heritability computation for family selections

h^2 for differences		Denominator	Variance Components in the Denominator			
			Genetic (also used in the numerator)			Error
			Coefficient for			
among "m" (m)	within "n" (n)	obtained from lines	σ^2_m	σ^2_f	σ^2_{mf}	σ^2_w
Full-sib	Plantation	2-5	JK(I-1)	IK(J-1)	K(IJ-1)	IJ-1
	Male	2-3	--	IK(J-1)	IK(J-1)	I(J-1)
	Female	2-4	JK(I-1)	--	JK(I-1)	J(I-1)
Half-sib						
Male	Plantation	3-5	JK(I-1)	--	K(I-1)	(I-1)
Female	Plantation	4-5	--	IK(J-1)	K(J-1)	(J-1)

In short, the generalized procedure for constructing heritability from analysis of variance is modified as follows:

1. Compute sum of square among genetic units as the denominator.
2. Identify variance components which will have contributed to the genetic gain.
3. Assemble these contributing variance components with their coefficients as the numerator.

The $h^2 = 1-(1/F)$ Approach

The basic concept of this unified formula is that all sources of variance within a genetic classification are considered as error as far as predicting gain from selection among such classification is concerned. For example, in a half-sib progeny test, 3/4 of the additive genetic variance and all of the dominance genetic variance present within family are useless for mother tree selection and are consequently included in the error term.

The F value for testing equality of means is a variance ratio: among-group variance divided by within-group variance. Therefore, the formula $h^2 = 1/(1/F)$ is:

$$h^2 = 1-1/(\text{MS group}/\text{MS error})$$

$$= \frac{\text{MS group - MS error}}{\text{MS group}}$$

$$= \frac{\text{Phenotypic Variance - Error Variance}}{\text{Phenotypic Variance Among Groups}}$$

$$= \frac{\text{Genetic Variance Among Groups}}{\text{Phenotypic Variance Among Groups}}$$

The steps in constructing this heritability are simply:

1. Calculate the F value suitable for testing the quality among groups.

2. Insert the computed F value and solve for $h^2 = 1-(1/F)$.

Most geographic variation studies fit the nested model and are useful here as an example. Stands (S_{ij}) are nested in different regions (R_i). Within-stand variation is considered to be environmental random error (E_{ijk}). We can express the model as:

$$Y_{ijk} = \mu + R_i + S_{ij} + E_{ijk}$$

The analysis of variance table is as follows:

Table 4.--Analysis of variance table for a nested design

Source	df	MS	F	EMS
Region	r-1	MS_r	MS_r/MS_s	$\sigma_e^2 + n\sigma_s^2 + sn\sigma_r^2$
Stand/Region	s-r	MS_s	MS_s/MS_e	$\sigma_e^2 + n\sigma_s^2$
Error	rsn-s	MS_e		σ_e^2
Total	rsn-1			

To compute heritability for regional difference, the F value to be used in the formula is obtained from MS_r/MS_s. By the same token, to compute heritability for stand difference within region, the F value is MS_s/MS_e.

Fixed and Random Models and Corresponding Heritability

Analysis of variance models may be classified as fixed, random, or mixed effect models. An effect is considered to be fixed if the researcher is interested only in the various levels of treatment used in his experiment. On the contrary, an effect is considered to be random if the researcher is interested in the population from which the treatments were drawn. The mixed effect model includes some treatments in fixed effects and some in random effects. An example using a multiplantation multiyear half-sib progeny test under various assumptions will help to interpret the heritability formula (table 5). For fixed effects the variance component represents variance among treatments in the experiment. For random effects the various components represent variance of the population from which the sample of treatments were drawn.

I. Fixed Effect: Mother Tree. Random Effect: Site and Year.

In this case we would be interested in selecting mother trees that would perform well on an average site through the years. The F test for mother tree is M/(MS + MY - MSY) (Kempthorne 1967). Substituting the expected mean square into the heritability formula, we have:

$$
\begin{aligned}
h^2 &= 1-1/F \\
&= (M - MS - MY + MSY)/M \\
&= \frac{Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}
\end{aligned}
$$

The interpretation of this formula is that all effects other than the mother tree are useless errors in selection.

Table 5.--Multiplantation and multiyear model for heritability computation (only the relevant EMS are listed)

Source	df	MSQ	EMS
Site	s-1	S	
Year	y-1	Y	
SxY	(s-1)(y-1)	SxY	
Mother tree	(m-1)	M	Ve+nVsym+nsVym+nyVsm+nsyVm
MxS	(m-1)(s-1)	MS	Ve+nVsym +nyvSm
MxY	(m-1)(y-1)	MY	Ve+nVsym+nsVym
MxSxY	(m-1)(s-1)(y-1)	MSY	Ve+nVsym
Replication	sy(n-1)	R	
Error	sy(n-1)(m-1)	E	Ve

II. Fixed Effect: Mother Tree and Site. Random Effect: Year

In this case we would be interested in selecting mother trees that would perform well on a specific site. The F test is M/MY. So we have:

$$h^2 = 1 - 1/F$$

$$= (M-MY)/M$$

$$= \frac{\frac{Vsm}{s} + Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}$$

Under this model both mother tree and mother tree x site interaction are genetic and useful, while error, mother tree x year x site and mother tree x year, are considered as non-genetic and useless.

III. Fixed Effect: Mother Tree, Site and Year

If the year effect is found to be related to some controllable factors (for example, amount of rainfall and pattern of rainfall can be simulated by irrigation), then we might be interested in selecting mother trees under a specific site and repeatable conditions. The F test in this model is M/E. So we have:

$$h^2 = 1 - 1/F$$

$$= (M - E)/M$$

$$= \frac{\frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s}}$$

The interpretation would be that of all the mother tree effect and its interaction with site and year are genetic and useful for selection.

Discussion and Conclusions

For a given model, both approaches yield an identical estimate of heritability. When the experimental design is balanced, the $h^2 = 1-(1/F)$ approach is recommended. The procedure is simple and useful for predicting genetic gain for the units being tested. The F-value is readily available from the analysis-of-variance table used for testing the quality of genetic unit means. There is no need to compute variance components and their coefficients, no worry about negative components, and no doubt about what goes into the heritability formula. However, the model that is being used and its implications must be thoroughly defined, and the F-value should be significant at a certain level. For example, it would be in error in a one-parent progeny test to consider families as fixed effects and then apply heritability and genetic gain values to the parent population. The concept of model effects and the appropriate F-value are more common than the expected variance components in most introductory statistics books (Li 1964, Ostle 1964, Bliss, 1967, and Daniel

1974). It appears to be easier for tree improvement workers to find the appropriate F-ratio than to determine which genotypic x environmental interactions should be included in the error term of the heritability formula.

If the experimental design is not balanced, the task of formulating a valid F-value may be as difficult as solving variance components. In an unbalanced design, the F-ratio and consequently the heritabiility is only an approximate value. Most provenance tests can be handled as nested analysis of variance with unequal sample sizes. Sokal and Rohlf (1969) gave two good examples in computing variance components and the approximate test of significance based on a reconstituted mean square.

The $h^2 = 1-(1/F)$ concept regards any repeatable effect present among genetic units as inheritable. For example, when testing wind pollinated progenies, the mother-tree effect includes not only the additive genetic contribution of the mother tree, but also the contribution of the wind-borne pollen as well as the extra chromosomal inheritance. On the other hand, this formula disregards any genetic variance within units. The variance components approach, by defining genetic and non-genetic variances, can demonstrate explicitly the definition of heritability (that portion of phenotypic variance due to genetic effects). However, the $h^2 = 1-(1/F)$ approach is functional for predicting gain in family, stand, and ecotype units.

The $h^2 = 1-(1/F)$ approach is restricted to the units being tested and selected, whereas the variance components approach is more flexible in estimating other related heritabilities. For example, in a progeny test, heritability of individual differences, useful in predicting gain in mass selection, can be constructed only by the variance components method.

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ANALYSIS OF VARIANCE CALCULATIONS FOR IRREGULAR EXPERIMENTS[1]

Jonathan W. Wright[2]

ABSTRACT.--Irregular experiments may be more useful than much smaller regular experiments and can be analyzed statistically without undue expenditure of time. For a few missing plots, standard methods of calculating missing-plot values can be used. For more missing plots (up to 10 percent), seedlot means or randomly chosen plot means of the same seedlot can be substituted for missing plots, provided between-block differences are small. Whatever the number of missing plots (provided there is more than one plot per seedlot) or the size of the between-block differences, seedlot means and sums of squares can be estimated in terms of deviations from block means. The procedures for calculation of analysis of variance in terms of deviations are described. The procedures are also applicable to regular experiments.

Ideally, a forest genetic experiment should follow a regular design in which each seedlot is represented in an equal number of blocks in every plantation. However, perfect regularity is rarely possible. There are usually a few missing plots as the result of mortality. Also, many times planting stock is more limited for some seedlots than for others. When that happens, one can plan a regular experiment by reducing the numbers of families and replications, or one can go ahead and distribute each family to each replication as long as the planting stock lasts. If the first alternative had been followed, most NC-99[3] experiments would have been reduced in size by 90 percent. Most NC-99 members probably agree that the second alternative was more desirable even though it resulted in experiments with great irregularities.

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[3] NC-99 is an organization of University and federal forest tree geneticists. The group has conducted cooperative provenance and progeny tests in northcentral United States for almost 20 years.

This paper has two objectives. The first is to present relatively simple methods to analyze data from experiments with various degrees of irregularity. The second is to allay frequently encountered fears of irregular data when planning experiments that might lose much information if made perfectly regular.

In using these methods, one must remember that the resulting analyses are only as strong as the data base. One can devise calculation methods to allow for missing data, but the inferences can never be as strong as if the data were not missing.

STANDARD PROCEDURE FOR CALCULATING MISSING PLOT VALUES

With a randomized complete block experiment in which seedlot A is missing from block 1, the standard procedure for calculating a substitute value is as follows (from Sokol and Rohlf 1969):

(1) Calculate all seedlot sums, block sums, and the overall sum, omitting the missing plot in each case.

(2) Calculate a missing plot mean as follows:

$$\text{Missing plot mean} = \frac{\text{Nb(Sum seedlot A)} + \text{Ns(Sum block 1)} - \text{Overall sum}}{(\text{Nb}-1)(\text{Ns} - 1)}$$

where Nb = number of blocks and Ns = number of seedlots.

(3) Using this substitute value, calculate the analysis of variance in the normal manner.

(4) Reduce the degrees of freedom for error by 1 for each missing plot.

If there is more than one missing plot, the first value must be calculated by using reasonable estimates for the other values, using the first value and reasonable estimates for all other values to calculate the second, etc. When there are many missing values, the preliminary estimates and calculated values may differ appreciably, in which case it may be necessary to redo some of the calculations.

This is the best way to calculate a missing-plot value, but is laborious if the number of missing plots is large.

USE OF SEEDLOT MEANS OR RANDOMLY CHOSEN PLOT MEANS

If the number of missing plots is small and there are minor differences among blocks, either of two simple procedures can be used. For each missing plot, one can substitute either (1) the mean for that seedlot, or (2) the mean of a randomly selected plot of the seedlot. In either case, reduce the degrees of freedom by 1 for each missing plot.

The first method changes seedlot means the least but the second is easiest to use with a computer.

The validity of these procedures can be checked by analyzing data from a completely regular experiment, eliminating some plots arbitrarily, substituting values for them, and re-calculating the analysis of variance. This has been done with several sets of data. Generally, there has been less than a 1 percent change in any mean square or F value as the result of substituting for up to 10 percent of the plot means.

Use of one of these simple substitution methods will normally cause less than a 2 percent change in the mean for an individual seedlot if only one or two plots per seedlot are missing and block means differ by less than 20 percent. Another calculation method may be preferable if there are more missing plots or large differences among blocks.

DISCARDING UNDER-REPRESENTED SEEDLOTS OR BLOCKS

If the missing plots are concentrated in a few seedlots or blocks, those seedlots or blocks can be eliminated to make the remaining data perfectly regular. This procedure is often satisfactory unless the incompletely represented seedlots are among the best.

ANALYSIS BASED UPON DEVIATIONS RATHER THAN TOTALS

Most students learn to do an analysis of variance by squaring the plot means, the seedlot sums, the block sums,etc. The analysis can be done, however, by working with the deviations of the plot means from the block means or seedlot means. By working with such deviations, one can avoid most of the problems encountered in irregular experiments.

Use of the deviation method requires transcription of a data array presented in terms of plot means to one presented in terms of deviations from either seedlot means or block means. This constitutes an extra step. However, subsequent computations are greatly simplified if the deviations are rounded off to the nearest whole number. Such rounding off is rarely of consequence. I often use deviations in preference to the standard method even when working with regular data arrays.

Adequacy of Deviations when Calculating Sums of Squares

Assume that one wishes to calculate the sum of squares and standard deviation of the series of 10 numbers included under column I in table 1. This can be done in either of two ways:

(1) Square each number as in column II. Find the total of the squares (280). Calculate the total for column I, square it and divide by 10 to obtain the correction factor ($50^2/10 = 250$). The "sum of squares" ($280 - 250 = 30$) is the total of the squares minus the correction factor.

(2) Determine the deviation of each number from the mean of 5.0, enter the deviations in column III, square them (column IV) and sum them to obtain a "sum of squares" of 30.

Notice that the two methods give identical results.

Table 1.--Example showing two ways of calculating the sum of squares of a series of 10 numbers

	I Actual	II Square of actual number	III Deviation of actual number from mean	IV Square of deviation
	2	4	-3	9
	3	9	-2	4
	4	16	-1	1
	4	16	-1	1
	5	25	0	0
	5	25	0	0
	6	36	+1	1
	6	36	+1	1
	7	49	+2	4
	8	64	+3	9
Total	50	280	0	30
Mean	5.0		0.0	
Correction factor		$50^2/10 = 250$		$0^2/10 = 0$
Sum of squares		30		30

Slight Effects of Small Arithmetic Mistakes or Rounding Off Errors

Assume that one makes a mistake of 1 when adding column I in table 1, obtaining a total of 49 instead of 50. The correction factor would then be calculated as $49^2/10 = 2{,}401/10 = 240.1$. The sum of squares would be calculated as $280 - 240.1 = 39.9$ instead of the true value of 30.

Assume also that a person made the same mistake when working with deviations, obtaining a total of +1 for column III. The correction factor would be calculated as $1^2/10 = .1$. The sum of squares would be calculated as 29.9 instead of 30.

Or, assume that the numbers are changed slightly to produce a total of 49 for column I in table 1. Rounding off the mean of 4.9 to 5.0 and the use of whole-number deviations would result in an error of 0.1 in the sum of squares.

Thus, even with the small deviations shown in table 1, rounding off errors are of little consequence. They are even less important with larger deviations. Also, when using deviations, small arithmetic mistakes may have negligible consequences.

Estimating Seedlot Means by Using Deviations from Block Means

Table 2 is an hypothetical data array showing how to calculate seedlot means by using deviations from block means. It was formulated by assuming a regular experiment with progressively greater growth from block 1 to 5 and from seedlot 1 to 9.

Table 2.--Example showing estimates of seedlot means when calculated from actual values and as deviations from block means for an experiment having many missing plots. (The example was formulated in such a way as to have theoretical means of 0, 7, 8....14 for seedlots 1 to 9, respectively and of 6, 8, 10, 12 and 14 for blocks 1 to 5, respectively, if there were no missing plots.)

Seed-lot no.	Actual values							Deviations from block means							Estimated means		
	Height in block					Sum	Mean	Height in block					Sum	Mean	The-ory	Act. val.	Devia-tions
	1	2	3	4	5			1	2	3	4	5					
1	2	4	6	--	--	12	4	-4	-4	-4	--	--	-12	-4	6	4	6.1
2	--	--	7	9	11	27	9	--	--	-3	-3	-3	-9	-3	7	9	7.1
3	4	6	8	10	12	40	8	-2	-2	-2	-2	-2	-10	-2	8	8	8.1
4	--	--	9	11	--	20	10	--	--	-1	-1	--	-2	-1	9	10	9.1
5	6	8	10	12	14	50	10	0	0	0	0	0	0	0	10	10	10.1
6	--	--	11	13	--	24	12	--	--	+1	+1	--	+2	+1	11	12	11.1
7	8	10	12	14	16	60	12	+2	+2	+2	+2	+2	+10	+2	12	12	12.1
8	--	--	13	15	17	45	15	--	--	+3	+3	+3	+9	+3	13	15	13.1
9	10	12	14	--	--	36	12	+4	+4	+4	--	--	+12	+4	14	12	14.1
n	5	5	9	7	5	31		5	5	9	7	5	31				
Sum	30	40	90	84	70	314		0	0	0	0	0	0				
Mean	6	8	10	12	14		10.1	0	0	0	0	0		0	10.0	10.1	10.1

The procedure is as follows:

(1) Calculate block totals and means as under "actual values".

(2) Calculate "deviations from block means" as in the central portion of the table.

(3) For each seedlot, add the average "deviation from block mean" to the plantation mean to obtain an estimated true mean (right-hand column).

While there is greater agreement between theory and practice in this hypothetical example than in actual practice, use of the deviations-from-block-means method always gives better estimates of seedlot means than can be obtained by averaging the actual plot means. The larger the number of missing plots and the greater the between-block differences, the greater the advantage of the deviation method.

Analysis of Variance Calculations Using Deviations from Block Means

To compute an analysis of variance, proceed as outlined below and in table 3.

Table 3.--Methods used to calculate means and analysis of variance for an irregular experiment, using deviations from block means (Sums of Squares and Degrees of Freedom are symbolized by SSQ and DF, respectively.)

Seed-lot	True means for block							Deviations from block means								Probable true
no.	1	2	3	4	5	Sum	Ave.	1	2	3	4	5	Sum	Freq.	Ave.	mean
1	A	A	A	-	A			G	G	G	-	G	J	n_s	K	K+E = L
2	A	-	A	A	-			G	-	G	G	-	J	n_s	K	L
3	-	A	A	A	-			-	G	G	G	-	J	n_s	K	L
4	A	A	-	A	A			G	G	-	G	G	J	n_s	K	L
5	A	-	-	A	A			G	-	-	G	G	J	n_s	K	L
6	-	A	A	-	A			-	G	G	-	G	J	n_s	K	L
S	B	B	B	B	B	D		H	H	H	H	H	M		Zero	D
Freq.	n_b	n_b	n_b	n_b	n_b	n_t								n_t		
Mean	C	C	C	C	C		E								Zero	E

G = A - C

$SSQ_{seedlot}$ = $\Sigma(J^2/n_s) - M^2/n_t = \Sigma(J^2/n_s)$, approximately

SSQ_{block} = $\Sigma(B^2/n_b) - D^2/n_t$, approximately

SSQ_{error} = $\Sigma G^2 - \Sigma(n^2/n_b) = \Sigma G^2$, approximately

$DF_{seedlot}$ = number of seedlots - 1

DF_{block} = number of blocks - 1

DF_{total} = total number of plots - 1

Arithmetic checks: each H and M should be less than $\pm n_b/2$ and $n_t/2$, respectively.

(1) For each living plot, enter a true mean (A) as in the left-hand portion of table 3. Calculate the sum, number of plots, and mean for each block (B, n_b and C, respectively) and for the entire plantation (D, n_t and E, respectively).

(2) Prepare a table similar to the right-hand portion of table 3. For each living plot enter a deviation-from-block-mean (G = A - C). Calculate the sum of deviations, number of plots and average deviation for each seedlot (J, n_s and K, respectively) and for the entire plantation (M, n_t and close to zero, respectively). Also, calculate the sum of the deviations (H) for each block.

(3) Check the arithmetic. If there are no mistakes, $\Sigma H = \Sigma J = M =$ less than $n_t/2$; $\Sigma n_b = \Sigma n_s = n_t$; and $\Sigma K =$ nearly zero. Also, each H and M should be less than $\pm n_b/2$ and $n_t/2$, respectively.

(4) For each seedlot calculate a probable true mean (L = K + E).

(5) Calculate the sums of squares (SSQ) and degrees of freedom (DF) as indicated at the bottom of table 3.

(6) Calculate mean squares (MSQ = SSQ/DF) and F values in the normal manner.

Analysis of Variance Calculations Using Deviations from Seedlot Means

If differences among blocks are small, the analysis of variance can be calculated in terms of deviations from seedlot means, using the methods outlined below:

(1) For each living plot, enter a true mean (A) as in the left-hand portion of table 4. Calculate the sum, number of plots (and mean) for each seedlot (F, n_s and L, respectively) and for the entire plantation (D, n_t and E, respectively).

(2) Prepare a table similar to the right-hand portion of table 4. For each living plot, enter a deviation-from-seedlot-mean. As an arithmetic check, calculate the sum (Q = less than $n_s/2$) for each seedlot.

(3) Calculate the sum of the deviations (P) for each block.

(4) Calculate the sums of squares (SSQ) and degrees of freedom (DF) as indicated at the bottom of table 4.

(5) Calculate mean squares and F values in the normal manner.

When differences among blocks are so small as not to be obvious in the field, they can be ignored in the analysis of variance calculations, often saving one-third in computation time. In this case, the signs of the deviations can be ignored and the P's need not be calculated. When the F ratio for block is less than 3.0, separation of the block from the error sum of squares usually has a negligible effect on the error term.

Table 4.--Methods used to calculate means and analysis of variance for an irregular experiment, using deviations from seedlot means. (Sums of Squares and Degrees of Freedom are symbolized by SSQ and DF, respectively. Except where otherwise noted, symbolism is the same as for table 3.)

Seed-lot	True means for block								Deviations from seedlot means						Deviation of true sum from expected sum
no.	1	2	3	4	5	Sum	Freq.	Ave.	1	2	3	4	5	Sum	
1	A	A	A	-	A	F	n_s	L	N	N	N	-	N	Q	$J = F - n_sE$
2	A	-	A	A	-	F	n_s	L	N	-	N	N	-	Q	J
3	-	A	A	A	-	F	n_s	L	-	N	N	N	-	Q	J
4	A	A	-	A	A	F	n_s	L	N	N	-	N	N	Q	J
5	A	-	-	A	A	F	n_s	L	N	-	-	N	N	Q	J
6	-	A	A	-	A	F	n_s	L	-	N	N	-	N	Q	J
Sum						D			P	P	P	P	P	M	
Freq.							n_t		n_b	n_b	n_b	n_b	n_b	n_t	
Mean								E							Zero

$N = A - L$

$SSQ_{seedlot} = \Sigma(J^2/n_s)$, approximately

$SSQ_{block} = \Sigma(P^2/n_b)$, approximately

$SSQ_{error + block} = \Sigma N^2$, approximately

$SSQ_{error} = SSQ_{error + block} - SSQ_{block}$

$DF_{seedlot}$, DF_{block}, DF_{total} = number of seedlots - 1, number of blocks - 1, and total number of plots - 1, respectively.

Arithmetic checks: each Q and M should be less than ± $n_s/2$ and $n_t/2$, respectively.

Analysis of Variance, Using Data from Several Plantations

The procedures when using data from several plantations are described below and in table 5:

(1) Start with single-plantation analyses as outlined in tables 3 or 4.

It is not necessary to use the same calculation method for all plantations.

Table 5.--Methods used to calculate means and analysis of variance for an irregular experiment involving several plantations, using deviations from plantation means as calculated by use of tables 3 or 4 (Symbolism is a continuation of that used in those tables.)

Seed-lot no.	Sum of deviations					Number of plots					Average deviation	Probable true mean
	Plantation 1	2	3	4	Sum	Plantation 1	2	3	4	Sum		
1	J	J	-	J	R	n_s	n_s	-	n_s	n_{sp}	$S = R/n_{sp}$	$U = S + T$
2	J	-	J	J	R	n_s	-	n_s	n_s	n_{sp}	S	U
3	J	-	-	J	R	n_s	-	-	n_s	n_{sp}	S	U
4	J	J	J	-	R	n_s	n_s	n_s	-	n_{sp}	S	U
5	J	J	J	J	R	n_s	n_s	n_s	n_s	n_{sp}	S	U
6	J	J	-	-	R	n_s	n_s	-	-	n_{sp}	S	U
Sum	Nearly Zero					n_t	n_t	n_t	n_t	n_{gt}		
Mean											Zero	T
						ACTUAL SUMS AND MEANS						
Sum	D	D	D	D	V							
Mean	E	E	E	E								$T = V/n_{gt}$

$SSQ_{\text{seedlot}} = \Sigma(R^2/n_{sp})$

$SSQ_{\text{seedlot + seedlot X plantation}} = \Sigma(J^2/n_s)$

$SSQ_{\text{seedlot X plantation}}$ is obtained by subtraction.

$SSQ_{\text{plantation}} = \Sigma(D^2/n_t) - V^2/n_{gt}$

$SSQ_{\text{block-within-plantation}}$ and SSQ_{error} are obtained by adding the SSQ_{block} and SSQ_{error}, respectively for the individual plantations.

DF_{seedlot} and $DF_{\text{plantation}}$ are the number of seedlots - 1, and the number of plantations - 1, respectively.

$DF_{\text{seedlot + seedlot X plantation}}$ = the sum of the DF_{seedlot} for the individual plantations; obtain $DF_{\text{seedlot X plantation}}$ by subtraction.

DF_{block} and DF_{error} = the sums of these for individual plantations.

If the measurements and analysis have been done by different individuals and in different units, a simple conversion is possible. If, for example, some plantations were measured in inches and others in centimeters, and all are to be converted to centimeters, all means and deviations based on inches should be multiplied by 2.54 and all sums of squares or mean squares based on inches should be multipled by $2.54^2 = 6.45$.

(2) Prepare a table similar to the left-hand portion of table 5 and insert a plantation-sum-of-deviations (J) and the number of plots (n_s) for each seedlot represented in any one plantation. For each plantation, insert the actual sum (D), actual mean (E) and total number of plots (n_t).

(3) For each seedlot, calculate the total sum-of-deviations (R) and average deviation ($S = R/n_{sp}$). For all plantations combined, calculate the actual sum (V), number of plots (n_{gt}) and mean (T).

(4) Calculate the probable true mean ($U = S + T$) for each seedlot.

(5) Calculate the sums of squares as indicated at the bottom of table 5. The sums of squares for error, block-within-plantation and "seedlot + seedlot X plantation" have already been calculated for individual plantations and may be summed to obtain the values for all plantations combined.

(6) Calculate degrees of freedom as indicated.

(7) Compute mean squares and F values in the normal manner.

LEAST SQUARES TECHNIQUE FOR USE WITH COMPUTERS

A least squares technique is available for those with access to a computer. This technique can be used with data such as are considered here. The analysis procedures are such as to stretch the capacity of even the largest computers. The routines are therefore effectively limited to experiments including a few score seedlots and a few plantations.

LIMITATIONS AND ADVANTAGES OF THE DEVIATIONS TECHNIQUES

With perfectly regular experiments, the deviations-from-means techniques yield exactly the same results as would be obtained with normal calculation procedures.

The standard method for calculating missing-plot values is laborious and therefore effectively limited to experiments with less than a few dozen missing plots. The simple substitution methods (seedlot mean or randomly chosen plot mean) are limited to experiments with small between-block differences and less than 10 percent missing plots. There are no such limitations to the use of the deviations-from-means techniques.

They can yield satisfactory results even if 50 percent of the plots are missing and there are large differences among blocks.

Whatever the calculation method, seedlots represented by a single plot in one plantation or in one plantation only in the case of a multi-plantation experiment should be excluded from an analysis of variance. Otherwise, the sum of squares due to seedlot will be inflated.

One situation is not amenable to the techniques described here: that in which certain blocks or plantations are composed primarily of seedlots considerably above or below average in the trait being measured. This might happen if seedlots of supposedly rapid growth are assigned to one series of plantations and seedlots of supposedly slow growth are assigned to other plantations. In such a case, there is a confounding of between-seedlot and between-block or between-plantation differences such that none of them can be estimated accurately.

Although the unequal sample sizes found in an irregular experiment do not pose serious problems in the calculation of analysis of variance or probable true means, they do in estimating the significance of a difference between any two means. Suppose that some seedlots are represented in 10 blocks and others in only 5 blocks. "Least Significant Differences" or multiple-range tests applicable to the former are not applicable to the latter. In such a case, means must be compared individually.

The deviations-from-mean techniques saves the most time in large experiments containing 100+ seedlots and several plantations, none of them complete. In such a case, the only reasonable alternative may be the exclusion of several seedlots or plantations from the analysis.

Even if few plots are missing, working with deviations can save time because of the lesser need for absolute accuracy in the computation work. As explained in connection with table 1, the smallest arithmetic mistake may have large consequences when working with true means and their sums of squares. That being the case, it is necessary to check every arithmetic operation until the slightest discrepancies are eliminated. Frequently, that requires much time. If working with deviations and their sums of squares, many slight arithmetic mistakes can be forgiven, so that much less cross checking is necessary.

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VARIATION IN MONOTERPENE CONTENT AMONG GEOGRAPHIC[1] SOURCES OF EASTERN WHITE PINE

A. R. Gilmore and J. J. Jokela

ABSTRACT.--Variations of monoterpenes in cortical oleoresins and foliar samples were determined for seed from 16 provenances of eastern white pine (Pinus strobus L.). The experiment was analyzed using the "raw" and the arcsine "transformed" data. Alpha-pinene, camphene, and β-pinene varied between seed sources when "raw" data were analyzed and α-pinine, β-pinene, and myrcene varied between seed sources when "transformed" data were analyzed. No trend was detected for latitude or longitude of seed origin for any monoterpene. Foliar monoterpenes did not vary among seed sources and no geographic pattern or trend was indicated for any monoterpene.

Previous studies have shown regional variation in the monoterpenes of certain coniferous species. For example, Gilmore (1971) found that α-pinene in loblolly pine increased almost linearly from the southernmost to northernmost seed source; Smith (1977) reported evidence to support the establishment of at least five regions and four transition-zone types of ponderosa pine; Hanover (1966) showed most of the variations in monoterpene content in western white pine to be genetically controlled; and Hilton (1968) found that the concentration of five monoterpenes in 23 geographic sources of eastern white pine varies, but he could not show distinct geographic patterns for these monoterpenes.

A range-wide provenance test of 16 sources of eastern white pine (Pinus strobus L.) planted in west central Illinois in 1959 provided an opportunity to study the relation between monoterpenes and

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geographic origin of white pine growing on a uniform site outside its natural range. The most southerly natural occurrence of white pine in the Mississippi River Valley is in northern Illinois, which is about 100 miles north of the plantation used in this study.

METHODS

Seed from 16 provenances of eastern white pine were collected by the U.S. Forest Service (table 1) and sown during the 1957 and 1958 growing seasons in the State Tree Nursery at Morgantown, North Carolina.

Table 1.--Origin of eastern white pine provenances

Location	North latitude	West longitude	Elevation in feet
Union County, Georgia (GA)	34°46'	84°03'	2450
Greene County, Tennessee (TN)	36°00'	82°48'	2250
Pulaski County, Virginia (VA)	37°05'	80°50'	2400
Monroe County, Pennsylvania (PA)	41°05'	75°25'	1800
Franklin County, New York (NY)	44°25'	74°15'	1600
Penobscot County, Maine (ME)	44°51'	68°38'	150
Ashland County, Ohio (OH)	40°45'	82°15'	1000
Allamakee County, Iowa (IA)	43°28'	91°30'	1000
Cass County, Minnesota (MN)	47°23'	94°25'	1300
Forest County, Wisconsin (WI)	45°51'	88°54'	1500
Newaygo County, Michigan (MI)	43°30'	85°40'	600
Algoma District, Ontario (ON)	46°10'	82°37'	650
Pontiac County, Quebec (PQ)	47°30'	77°00'	1000
Lunenburg County, Nova Scotia (NS)	44°25'	64°35'	150
Transylvania County, North Carolina (NC)	35°14'	82°38'	2120
Greenbrier County, West Virginia (WV)	38°02'	80°30'	2600

In 1959, 2-0 seedlings of all provenances except Michigan were planted in 4-tree row plots, replicated 12 times. Seedlings from the Michigan source were planted in 1961 as 2-1 stock. The experimental trees were spaced 7 feet apart, in rows 14 feet apart. White pine seedlings planted in intervening "filler" rows were removed after the 1970 growing season. The plantation is located in the "sand hill" area of west central Illinois in Cass County. The soil type is a Plainfield fine sand (Typic Udipsamments) and is fairly uniform over the planted area. Growth and survival data have been obtained periodically; the last measurements were taken in the fall of 1973. Survival at the end of the first growing season ranged from 52 to 90 percent. Fail spots were replanted in 1961 with surplus stock (2-2) that had been grown an additional 2 years in the Mason State Tree Nursery in Illinois. Survival of provenances after the 1973 growing season ranged from 90 to 100 percent and averaged 97 percent.

The plantation was thinned to two trees per plot in December, 1974, when it was 16 years old. The uncut trees represented the best of the largest trees. Before the plantation was thinned, a cut was made through the bark at breast height on 8 to 10 sample trees per provenance. The oleoresin exuding from each cut was collected in a small vial, which was placed on ice for transport to the laboratory where the sample was frozen until it was analyzed.

Foliar samples were taken from the upper part of the crown of each sample tree when felled. The needles were placed in plastic bags in an ice cooler for transport to the laboratory where they were frozen until analyzed.

Cortical oleoresin samples were dissolved in hexane containing 670 ppm cumene and this solution was analyzed for monoterpenes. Each monoterpene was computed as percentage of weight of the oleoresin sample, using cumene as the internal standard.

Monoterpenes in the foliar samples were determined by injecting a solid segment of needle without cumene into the gas chromatograph, as described by Roberts (1968). The content of each foliar monoterpene was expressed as a percentage of the total monoterpene concentration in the sample. Otherwise, analytical procedures were the same as those for the cortical oleoresin samples.

Samples were analyzed with a Hewlett-Packard Model 5750 Gas Chromatograph equipped with dual hydrogen-air ionization detectors using stainless steel columns with 20 percent carbowax 20M liquid phase on 60-80 mesh, acid-washed chromosorb W solid support. Operating conditions were: injection port, 200°C; detector 225°C; column 110°C; and He flow 17 cm^3/min.

The raw data were statistically analyzed as a complete randomized design, and differences between provenances for each significant variable were determined by the least-significant-difference method. In addition, the raw data of the monoterpenes in the cortical oleoresin samples were transformed using an arcsine function and analyzed as were the raw data.

RESULTS AND DISCUSSION

The average height and diameter (d.b.h.) of sample trees according to seed source are shown in Table 2. The average height of all sample trees was equal to the plantation average (26 feet), whereas the diameter of cut trees was slightly smaller than the plantation average - 5.0 vs. 5.3 inches. Differences in average height or average diameter between sample and all trees in a seed source was small, never exceeding 2 feet in height or 0.6 inches in diameter. Therefore, the sample trees were considered to be reasonably representative of the plantation.

Table 2.--Average heights and diameters (d.b.h.) of sample trees at end of 1973 growing season by seed source

Seed source	Height[1]	Seed source	Diameter[1]
	feet		inches
GA	31	TN	6.4
TN	29	GA	6.2
NC	29	PA	5.8
PA	29	OH	5.7
WI	27	NC	5.6
MI	27	MI	5.5
OH	27	WI	5.2
NS	26	WV	5.0
WV	26	NS	4.9
MN	25	MN	4.9
ON	25	VA	4.5
NY	25	PQ	4.5
VA	24	ON	4.5
PQ	23	NY	4.3
IA	20	ME	3.6
ME	19	IA	3.6
Average	26	Average	5.0

[1] Any two averages not included within the same line appearing to the right of each ranking of source are significantly different at 5-percent level.

Six monoterpenes were found in the cortical oleoresin of all seed sources. The order in which they eluted from the gas chromatographic column were α-pinene, camphene, β-pinene, myrcene, limonene, and β-phelledrene. Hilton (1968) reported two additional monoterpenes in eastern white pine than were reported in this study: 3-carene and terpinolene. This discrepancy can be explained by the fact that 3-carene was eluting from the gas chromatographic column at the same time as our marker cumene and could not be detected. This resulted in the amount of cumene appearing greater under the curve on the chromatogram chart than its actual amount. Therefore, an error might have been introduced in computing the quantities of monoterpenes in a sample. But when we determined the monoterpenes in a number of our cortical oleoresin samples without using cumene, we found that the concentrations of 3-carene was low when compared to the other monoterpenes in the sample and in some samples it was not detected. So, we feel confident that our conclusions from this study are valid and would not change, even if some other marker was used that would not interfere with the monoterpenes eluting from the gas chromatograph. We did not report terpinolene in the study as it was detected in only a few samples and the incidence was too small and varied among seed source to be considered.

The composition of those monoterpenes in cortical oleoresins that varied significantly among seed sources and the ranking of these sources is shown in Table 3. Although significant differences were found between provenances for α-pinene, camphene, and β-pinene when the raw data were analyzed, no distinct geographic concentration pattern was established because no significant correlation was found between latitude or longitude of the seed source and any of the monoterpenes in the oleoresin. These results agree with Hilton (1968) who did not establish a monoterpene pattern for eastern white pine. But it is interesting to note that the New York seed source had the highest concentration of camphene and β-pinene and the next to highest concentration of α-pinene. On the other hand, the Ohio seed source had the lowest concentration of camphene and β-pinene but was average in its concentration of α-pinene. The raw data averages of the three monoterpenes that did not differ among seed source were: myrcene, 2.5; limonene, 0.1; and β-phelledrene, 0.8.

When the raw data of cortical oleoresin was converted using arcsine transformations, the analyses showed that α-pinene, β-pinene, and myrcene varied significantly among seed sources at the 5-percent level, whereas camphene differences only approached significance at this level (table 4). But the relative rank of seed sources for each monoterpene was almost the same regardless of the method of anlaysis used (raw data or transormation).

There were some tree-to-tree variations in the composition of the monoterpene fractions in the cortical oleoresin, not only for all trees but also for trees within a seed source. Similar results have been shown by numerous investigators for other tree species.

The average concentrations and range of monoterpenes in the foliage are shown in table 5. Foliar monoterpenes varied widely among trees and there was no significant difference between seed sources and no geographic concentration pattern or trend was indicated. It would have been interesting from an academic viewpoint to determine the chemical composition of the four unknown monoterpenes. But because of the findings in this phase of the study, the time and expense could not be justified at this time.

CONCLUSION

Although we found distinct differences in some cortical monoterpenes between provenances, white pine does not seem to exhibit a distinct geographic concentration pattern for any of the detected monoterpenes. As shown in this and other studies, cortical and foliar monoterpenes vary widely between trees within a seed source.

Table 3.--Ranking of white pine sources by average percentages of raw data of α-pinene, camphene, and β-pinene in cortical oleoresin samples1/

α-pinene		Camphene		β-pinene	
Source	Oleoresin	Source	Oleoresin	Source	Oleoresin
	Percent		Percent		Percent
PA	8.11	NY	1.28	NY	8.41
NY	7.09	ME	1.20	WV	6.96
WV	6.36	WV	1.11	MN	6.70
ME	6.25	PA	1.09	ON	6.68
PQ	5,83	GA	1.03	NC	6.12
MN	5.70	IA	0.94	IA	6.09
OH	5.64	PQ	0.93	VA	5.95
TN	5.60	MN	0.92	PQ	5.93
GA	5.38	NC	0.91	TN	5.88
ON	5.29	TN	0.87	GA	5.59
NC	4.80	ON	0.85	WI	5.37
NS	4.61	MI	0.85	MI	4.97
WI	4.55	WI	0.73	ME	4.92
IA	4.47	NS	0.66	PA	4.69
VA	4.22	VA	0.60	NS	4.57
MI	3.98	OH	0.60	OH	1.88
Average	5.49	Average	0.91	Average	5.66

1/ Any two averages not included within the same line appearing to the right of each ranking of source are significantly different at 5-percent level.

Table 4.--Ranking of white pine sources by average percentages based on transformed data of α-pinene, β-pinene, and myrcene in cortical oleoresin samples 1/

α-pinene		β-pinene		Myrcene	
Source	Oleoresin	Source	Oleoresin	Source	Oleoresin
	Percent		Percent		Percent
PA	7.7	NY	7.8	OH	7.6
NY	7.0	MN	6.5	PA	6.2
ME	6.0	WV	6.3	WV	5.8
WV	5.9	IA	5.9	MI	2.8
PQ	5.7	NC	5.8	NS	2.9
MN	5.7	TN	5.7	NC	2.5
OH	5.6	PQ	5.7	TN	2.0
TN	5.5	VA	5.6	VA	1.7
GA	5.1	GA	5.3	WI	1.8
ON	5.1	ON	5.2	IA	1.6
NC	4.6	WI	4.9	ME	1.6
WI	4.4	MI	4.8	PQ	1.2
NS	4.4	ME	4.7	NY	1.2
IA	4.4	PA	4.3	GA	0.6
VA	4.1	NS	4.1	MN	0.6
MI	3.9	OH	1.7	ON	0.4
Average	5.3	Average	5.3	Average	5.7

1/ Any two averages not included within the same line appearing to the right of each ranking of source are significantly different at 5-percent level.

Table 5.--Monoterpene content of foliar oleoresin for 16 geographic sources of eastern white pine (raw data)

(In percent)

Terpene	Range of source means	Average of source means
α-pinene	4.7 - 10.3	6.8
Camphene	53.6 - 65.6	59.0
β-pinene	5.0 - 18.0	12.4
Myrcene	16.6 - 23.3	19.4
Limonene	5.2 - 13.3	8.7
Unknown 1	1.0 - 10.7	5.3
Unknown 2	1.0 - 3.5	1.8
Unknown 3	1.0 - 7.0	2.1
Unknown 4	3.4 - 8.7	5.5

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THE YELLOW X PAPER BIRCH HYBRID--A POTENTIAL SUBSTITUTE FOR YELLOW BIRCH ON PROBLEM SITES

Knud E. Clausen[1]

ABSTRACT--Yellow x paper birch hybrids and yellow birches with common female parents were compared after 5 growing seasons in an open field. Survival of the hybrids was 91 percent compared with 64 percent for the yellow birch trees. The hybrids were from 25 to 32 percent taller than the yellow birches and had 19-40 percent greater diameter. Because this hybrid not only grows better than yellow birch but also withstands greater environmental stress, it appears suitable for planting on open or partially shaded sites where ecological conditions are less favorable for yellow birch.

Natural interspecific hybridization is common in the genus Betula but natural hybrids between yellow birch (B. alleghaniensis Britt.) and paper birch (B. papyrifera Marsh.) have only been reported from Iowa, Minnesota, Wisconsin, Michigan, and New Hampshire (Clausen 1973b, Barnes et al. 1974). However, hybridization between these species apparently does occur over much of the range of yellow birch. When we grew yellow birch seedlings for a range-wide provenance study, yellow x paper birch hybrids appeared in 32 out of 55 seed sources. The sources with hybrids came from 13 states and 4 Canadian provinces ranging from Newfoundland to Minnesota and from Quebec to Georgia (Clausen 1973b). Because the hybrid seedlings grew faster than the yellow birch seedlings in the nursery, I decided to test this hybrid against yellow birch and to try to determine its potential as a possible substitute for yellow birch on certain sites.

METHODS

In the spring of 1972, when a yellow birch progeny test was established near Lake Tomahawk in Oneida County, northcentral Wisconsin, a number of yellow x paper birch hybrids were included. The seedlings for the progeny test were grown in a nursery at Rhinelander, Wisconsin, as previously described (Clausen 1973a), and planted in the field when 4 years old. The test site, a former potato field and pasture on Padus sandy loam, was kept clean-cultivated through the summer of 1975 and later mowed. The plantation included 144 yellow birch families in a split-plot design with 6 or 8 replications and hybrid trees of 3 families in 1, 5, and 12 replications, respectively. All families were set out in 4-tree plots and at 8 x 8 ft. spacing. From 1 to 3 hybrid trees of 13 additional families were planted in the border rows of the plantation. Two of these families were from Canadian sources that had not produced hybrids when used in the provenance test.

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Height and diameter at one-half tree height were measured after 5 growing seasons in the field. This paper is mainly concerned with those hybrid and yellow birch groups that had female parents in common and were growing together in the same replications. Because suitable yellow birch comparison plots were not available for about one-half of the hybrid plots and 13 of the hybrid families, these plots were not used in the analyses but did provide supporting information.

RESULTS

Previous publications reported the performance of the yellow birch families included in the progeny test after 4 years in the nursery (Clausen 1973a) and after 3 years in the field (Clausen 1975) but did not include any information about the performance of the hybrids. By the same token, the major portion of the 5-year yellow birch data will be presented elsewhere.

All trees in the hybrid plots with useable comparison plots were alive at the end of the fifth growing season in the field and only two comparison trees in one yellow birch family had died. Survival of all hybrids in the plantation was 91 percent compared with 64 percent for the yellow birch trees used as comparison trees or growing adjacent to the hybrids. Thus, the yellow x paper birch appears to survive better than yellow birch when planted under open field conditions.

Most hybrids followed the trend observed earlier in the nursery, and were still growing faster than yellow birch after 5 years in the field. The yellow birch comparison families averaged 174 cm in height compared with 221 cm for the hybrids (table 1). Of the individual families, hybrid group 2964-5, on the average, was 25 percent taller than its comparison group. A t-test showed that this difference was significant at the 0.5 level. The superiority in individual blocks ranged from 15 to 34 percent. Similarly, the superiority of the hybrids over the related yellow birches in family 2983-1 ranged from 8 to 60 percent and averaged 28 percent. This difference was not significant according to the t-test, probably because the differences between hybrids and yellow birch were small in 2 of the 4 blocks. The single plot of hybrid family 2983-10 was 32 percent taller than the yellow birch plot (table 1).

Table 1.--Mean height and diameter of yellow birch and yellow x paper birch hybrids after 5 years in the field

Family	Type of birch	No. of plots	Mean height	Percent superiority		Mean diameter[1/]	Percent superiority	
				Mean	Range		Mean	Range
			cm			mm		
2964-5	Yellow	4	172	--	--	13.6	--	--
	Hybrid	4	214*	25	15-34	16.1	19	4-36
2983-1	Yellow	4	176	--	--	13.1	--	--
	Hybrid	4	226	28	8-60	16.2*	24	3-31
2983-10	Yellow	1	174	--	--	11.4	--	--
	Hybrid	1	230	32	--	15.9	40	--
Means:	Yellow birch		174			13.1		
Means:	Hybrid		221			16.1		

[1/] Measured at one-half tree height.

* Difference between yellow birch and hybrid is significant at .05 level (t-test).

When additional hybrid plots of families 2964-5 and 2983-1 and of 12 other families were compared with unrelated yellow birches in adjacent plots, the hybrids were taller in 18 plots, of equal size in 1 plot, and smaller than yellow birch in 5 plots. So in general, the yellow x paper birch hybrid does have faster height growth than yellow birch does.

Tree diameter followed a pattern similar to that for tree height. The yellow birch families in the 9 comparison plots averaged 13.1 mm in diameter at one-half tree height as against 16 mm for the hybrids (table 1). Hybrid group 2983-1 had a significantly greater diameter than its comparison trees with an average superiority of 24 percent and a range between blocks from 3 to 31 percent. The diameter of hybrid plot 2983-10 was 40 percent greater than that of the yellow birch comparison plot. In the comparisons between hybrid plots and unrelated yellow birches, the hybrids had greater diameter in 21 plots, were of equal size in 1 plot, and had smaller diameter than yellow birch in 2 plots. Thus, the hybrid also has better diameter growth than yellow birch in most cases.

The superiority of the hybrid over yellow birch was also evident when single trees were compared. The tallest tree in a hybrid plot (family 2964-5) was 330 cm while the tallest yellow birch in a comparison plot (family 2983-1) measured 280 cm. This is a difference of 18 percent. In addition, the tallest tree per plot exceeded 200 cm in all of the 15 surviving hybrid groups, whereas only 5 of the yellow birch families had trees 200 cm and above. Although the greatest mid-tree diameter observed, 25 mm, was the same for both the hybrid and for yellow birch, nine hybrid groups had trees with diameters 15 mm and above, while only four yellow birch families had trees in this class.

DISCUSSION

The fact that hybrid seed is produced by yellow birch parent trees over much of the range of yellow birch (Clausen 1973b), indicates that hybridization between yellow birch and paper birch can take place whereever the two species occur together. The relative scarcity of reported hybrids may mean that the hybrids have difficulty getting established under natural conditions due to lack of suitable seedbeds and to competition from other plants. The 20 hybrids located by Barnes et al. (1974) were all growing in disturbed habitats which would have had exposed mineral soil, abundant light and little competition at the time of establishment. These authors also suggested that the hybrids were most likely to be found on mesic or wet-mesic sites. This is not too surprising because most hybrids have been found growing in association with yellow birch which typically occurs on such sites. However, the results of this study show that the hybrid can survive and grow very well on a much drier site. One could, in fact, expect such a possibility because the other parent of the hybrid, paper birch, is a pioneer species capable of growing on a wide range of sites, including fairly dry ones (Fowells 1965).

Open-field sites such as the one used in this test may not provide the best conditions for the growing of yellow birch but apparently are well suited for the hybrid. On such sites, control of competing vegetation is fairly easily accomplished and undoubtedly benefits both species. The abundance of light on open field sites appears to favor the hybrid, whereas our experience indicates that yellow birch will grow better under some degree of shade. The hybrid will also withstand greater environmental stress than yellow birch. Many trees in this plantation were left in a weakened condition at the end of the 1976 growing season due to a severe drought during the summer and fall. A light snow cover over the winter followed by hot, dry weather during May 1977 lead to further tree mortality so that only 78 percent of the hybrids and 35 percent of the yellow birches used in the comparisons were alive in June of that year.

Although the natural hybrid has shown better growth than yellow birch, it may not be superior to its other parent, paper birch. There were no paper birch trees included in this plantation so a direct comparison is not possible in this case. However, hybrids from controlled crosses between the two species have been grown and compared with trees of both parent species. In those tests, the hybrids again were faster growing than yellow birches of the same age, but were either slower growing or, at best, grew as fast as paper birch (Clausen 1973b).

The superior growth of the yellow x paper birch hybrid and its greater ability to survive in the open suggests to me that this hybrid would make a good tree to plant in places where the ecological conditions are less favorable for yellow birch. In other words, the hybrid could be planted in open or partially shaded areas where it could take advantage of the high degree of insolation and still would be able to tolerate the drier site. So far we don't know what the wood characteristics of the hybrid are but assuming that they are similar to those of yellow birch, the proposed use of the hybrid would enable us to grow a tree resembling yellow birch on a wider range of sites.

How then can one obtain planting stock of this hybrid? Although it is not difficult to recognize the hybrid in nursery beds of yellow birch, this method is impractical because less than 1 percent and rarely as much as 10 percent of the seedlings are usually hybrids (Clausen 1973b). A much more efficient way is to use controlled pollination. This is most easily carried out on grafted trees in the greenhouse but can also be done in the field. Yellow birch females should be pollinated with paper birch pollen because the chance of success and the yield of good seed is poorer when the cross is made in the opposite direction (Clausen 1970). Seed yield from yellow x paper birch crosses is about as good as that of open-pollinated yellow birch where it typically ranges from 150 to 200 seeds per catkin or occasionally higher. The hybrid seed tends to be of pooer quality than that of yellow birch but usually averaged about 50 percent germination. Because even a small yellow birch graft can have 10 to 20 female catkins, it is thus possible to produce a large amount of hybrid seed with relatively little effort.

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PREFACE

In May, 1975, a symposium was conducted in Tucson, Arizona, on the management of forest and range habitats for nongame birds. That landmark meeting brought together avian ecologists and resource managers. It was widely agreed that both groups benefited each other, and that a series of regional workshops should be held. The objective of the series would be to insure that nongame bird habitat requirements are considered in significant land management practices, and that a diversity of natural biological communities are maintained.

To that end, the National Nongame Bird Steering Committee was formed to sponsor regional workshops to present the state-of-the-art of nongame bird research and management in various ecoregions of the United States. The first workshop in the series was held in Portland, Oregon, February 7-9, 1977, entitled, "Nongame Bird Habitat Management in the Coniferous Forests of the Western United States".

A second workshop in the series, "Management of Southern Forests for Nongame Birds", held January 24-26, 1978 in Atlanta, Georgia, presented bird habitat research results and management techniques for all major habitat types in the southern and southeastern United States. This third workshop is jointly hosted by the USDA-Forest Service--the Eastern Region; Northeastern Area, State and Private Forestry; and the Northeastern Forest Experiment Station; and the Northcentral Forest Experiment Station.

The Forest Service was joined by the National Nongame Bird Steering Committee in sponsoring this workshop. Its members include:

Forest Service, USDA
Soil Conservation Service, USDA
Fish and Wildlife Service, USDI
Bureau of Land Management, USDI
National Wildlife Federation
The Wildlife Society
Wildlife Management Institute
National Audubon Society
International Association of Wildlife Conservation Agencies

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Tuesday Morning, January 23

BIRDS IN FOREST ECOSYSTEMS

Moderator: Roger Holmes
Minnesota Department of
Natural Resources

MANAGEMENT OF NORTHCENTRAL AND NORTHEASTERN FORESTS FOR NONGAME BIRDS

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Foresters have begun to recognize their responsibilities for nongame birds, but that concern must manifest itself through professional management rather than preservation. The key to success will be diversity of habitats, which can only be achieved with advanced planning and knowledge acquired through research.

Four years ago, I participated in the first National Symposium on the Management of Forest and Range Habitats for Nongame Birds. The same thing that impressed me then impresses me now. As I told that audience in Tucson, the most significant thing about that symposium was its being--the fact that there was a national symposium on nongame birds. It was a first--a milestone in forestry-wildlife relationships. As John Gottschalk pointed out, this was the "opening skirmish in a revolution." "History will record what has been said here and by whom," I told the group, "and I am proud to have a small part in it."

That symposium in 1975, as well as this workshop today, represent a long-overdue recognition of our responsibility for all living creatures. But, as I told that audience then and will say again, let's meet our responsibilities fully and enthusiastically, but let's not allow this concern for nongame birds to play into the hands of those who would deny the use of all renewable resources

There is a growing and widespread philosophy that would prohibit the taking of any wild species, even the cutting of trees. This "reverence of life" philosophy is sincere and well-meaning, but it is a misdirected effort that will not achieve what its proponents seek. Nothing is so sure as the dynamics of nature. Change is inevitable. We can slow down, speed up, or guide that change, but we cannot arrest it at any given point in time. Preservation, as many would apply it, is actually counterproductive to those values they cherish most. We, as professionals, must preach the doctrine of "wise use" and resist the growing movement that would deny wildlife harvest to all and place most public forests into preserves and refuges.

As a forester, I am proud to see my fellow professionals taking an active role in this workshop. It shows a concern that we all feel even though it might now have been too evident in the past. Here are rough-and-tumble woods foresters talking about songbird habitats. That's progress!

Foresters have learned many valuable lessons, but, admittedly, have made many mistakes in the past. We are concerned about all wildlife, about the total ecosystem, about game and nongame species alike. We will not repeat mistakes of the past--massive clearcuts, careless logging, destruction of fragile sites. Forestry operations of the future will avoid unstable soils, high alpine types which cannot be quickly and successfully regenerated, and damages to streams and watersheds.

Recently, I heard an industrial forester describe most clearcutting of the past as "commercial hygrading," characterized by standing cull trees, broken trees, worthless species, and a tangle of logging slash. No wonder there has been great public outcry about this kind of clearcutting! His own operation in West Virginia utilizes total tree chippers--everything is used. It is a clean operation ready for replanting or natural regeneration. Maximum size of any clearcut is 25 acres and all are fitted into the landscape in an irregular pattern.

Even-aged management is good silviculture for both hardwoods and conifers. It has a definite place in our forestry future, but it must be less offensive and better planned than much of what we have seen in the past.

How do I see the role of the resources professional in nongame bird management? Essentially the same as his role in timber management or wildlife management for game species. I have been outspoken on this subject in the pages of American Forests, so this will not be new to most of you. But, here is my formula:

1. Probably the greatest need is diversity. We must provide and maintain variety of habitats. The importance of edge is well known to game managers, and it has equal value to nongame species. Too much of anything is not good, for man nor beast. I sympathize with those who express growing alarm over pine monoculture in the South or massive clearcuts in the West. Yet, I support judicial application of both practices. There is truth in the old Chinese proverb that the "excess of any virtue is a vice." Let's retain all management practices in our arsenal of tools, but let's maintain variety in their application.

2. The key to diversity and variety is planning. If we want to benefit nongame birds we must plan for their habitats. Too much of our resources planning in the past has been single purpose, for trees or game species, seldom for both, and almost never for the total ecosystem, including nongame birds. Opportunities are almost unlimited if forestry and wildlife professionals provide for all resources in their initial planning, not as an afterthought, but as equal partners in objective.

3. The key to planning is knowledge, or facts, and the only way to acquire them is through research. What do we know about nongame bird habitats? A lot more than we apply, I am sure, but not enough. The thing we don't know is how to optimize timber management, game management and nongame management, all on the same lands at the same time. Foresters have done excellent research on silvicultural methods to maximize timber production. Bioligists are experts on ideal habitats for game species. And, I am sure we know a lot about nongame birds, but what do we know about the combinations? How much research has been done in northern forest habitats for renewable resources in total? Too little, I'm afraid, but I hope this workshop proves me wrong.

So my formula is diversity, planning and research. Until we achieve all three, nongame bird habitat management will be largely token or accidental. Sure, we will continue to burn some jack pines for the kirtland warbler, but what are we doing elsewhere? Do we really know what to do? There's a book I have been wanting to read on the passenger pigeon by A. W. Schorger. Everything I have heard about this vanished species was that we slaughtered them to extinction when they migrated in vulnerable flocks. According to Schorger, however, harvest had little to do with the disappearance of the passenger pigeon. We destroyed him when we changed his habitat. Maybe we created favorable habitat for another species, but wouldn't it be better if we had known before we did it? To me, that's what this workshop is all about. We've got to find better ways than we have used in the past. And, we have got to instill in all resource professionals a real sense of obligation and responsibility to all creatures, large and small, game and nongame, and nonprofitable as well as those that make us money.

Perhaps you have noted the overtone of professionalism I have injected in this keynote speech from the beginning. That is the one thing we must defend with all our strength. If we do not do our job as professionals, properly, we will lose the opportunity. The wave of preservation I spoke about earlier is born of fault and neglect. The protectionist is not pleased with our past performance. What he fails to realize, however, is that there is no substitute for applied management that only a professional can supply. What he seeks cannot be achieved by a "hands off" directive. His protective love can destroy the very thing he wants to preserve. But, we've got to convince him by action, not words. If we fail, then resource management decisions will be made by courts, by legislators, and in the ballot box rather than on the ground, the only place they can be made properly.

It should be obvious to all of you that I am not a nongame bird expert. I have little to offer this workshop except encouragement and motivation. Since I retired three weeks ago, I probably have lost any influence I might have had on legislation and appropriations. But, if I have a message it is a plea for tolerance and professional responsibility. Let's respect the beliefs and concerns of others, but let's also make sure we get our own house in order. There is a job to be done in recognizing, protecting, and improving the habitats of nongame birds. Let's be sure we do it, and do it right, or someone else will take over.

THE IMPORTANCE OF BIRDS IN FOREST COMMUNITIES

Richard L. Plunkett[1]

Abstract.--The usefulness of bird populations as monitors of the diversity of natural biological communities and to provide feedback to the manager as to the results of management programs is reviewed. Certain characteristics that contribute to the usefulness of birds as indicator species are discussed, and the need for reorientation toward ecosystem management in place of single-species management is stressed.

INTRODUCTION

When Richard M. DeGraaf prevailed upon me to accept this assignment, I was struck by the all-encompassing nature of the title of this paper, which is rather like the intellectual arrogance displayed by one of my professors at Northwestern University who published a book entitled simply "Man and his Works." He was an anthropologist, rather than an ecologist, which may offer an explanation though not an excuse. While it is true that ecologists are supposed to know how everything connects with everything else (Barry Commoner's First Law of Ecology), addressing this subject from a truly comprehensive standpoint lies way beyond my capabilities, and therefore I looked for a point of attack that would serve to simplify this paper and make it useful for the land manager.

One possible point of attack was that of the economic importance of birds in forest communities. The more I looked at this approach, the more difficult became the problem of how to quantify ecologic functions. That did not work.

A second point of attack would be to attempt to trace the cycling of energy through birds in forest ecosystems. Although this approach ultimately promises to be extremely useful, there is a real difficulty in drawing generalizations from the current studies that, given the present state of the art, must be restricted to relatively small plots in carefully delimited and relatively homogeneous habitats, so that this approach did not appear to offer anything of immediate practicality to the land manager.

A third point of attack would be to look at the importance of birds in forest communities in terms of their feeding ecology and its relation to insect population dynamics, perhaps examining the frequently cited role of birds in regulating the severity of outbreaks of defoliating insects. That looked promising, but when I reviewed those studies cited by Nisbet (1971), Wiens (1975) and Thomas et al. (1975), I found the evidence very much mixed. Briefly, it is apparent from those studies that birds consume only a small fraction (on the order of 1 to 7 percent, rarely as high as 14 percent) of defoliating caterpillars during the summer when insects are abundant, so that birds cannot be effective in controlling insect outbreaks in summer. Those studies also indicate, however, that birds may be capable of playing a substantial role in controlling insect populations in winter when the insects are sedentary. There are a number of studies indicating that in the winter birds may consume a much higher fraction (50 percent or more) of the insects found in a given area and thus could function to limit the number of insects emerging in the spring and hence to reduce the severity of summer outbreaks. Thus far, so good, but when I attempted to apply these findings, which are to a large measure based on European studies conducted in relatively small woodlots or on studies conducted in California and the Southwest, I noted that many of the insectivorous birds of our north central and northeastern forests are migratory and hence absent from our forests during the winter. In North America those species that depend on insects for food during the summer are the warblers, vireos, flycatchers, cuckoos, tanagers and chickadees, whereas the birds that depend on insects for food in the winter appear to be mainly the chickadees, nuthatches and woodpeckers. Where does this take us, except perhaps to emphasize the need for more intensive study of the feeding ecology of birds wintering in our forests, which may be useful but does not appear to be a particularly rewarding point of attack for this paper.

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This process of elimination left me with the approach for this paper that probably springs most naturally from my own work on behalf of the National Audubon Society---that of looking at bird populations, and especially at changes in bird populations, for what they can tell us about what is happening to the habitats on which they depend. Thus what I want to suggest in the remainder of this paper is that, to the land manager, the immediate importance of birds in forest communities may lie not in any of the ways of looking at birds outlined above, but rather that it may lie in the usefulness of birds as monitors of the diversity of natural biological communities, the habitats that the land manager is charged with preserving and enhancing.

USEFULNESS OF BIRDS AS MONITORS

If one reviews the Proceedings of the Symposium on Management of Forest and Range Habitats for Nongame Birds held at Tucson, Ariz., May 6-9, 1975, one will find a common, even dominant theme running through many of the symposium papers. This is that our lack of knowledge of the complex relationships, the interconnections, the interactive pathways of trophic web organization makes it extremely difficult for the land manager to manage habitats from a sound ecological approach. Now this is a valid statement, up to a point, but what I would like to suggest is that we may well turn the equation around, that we may look to the usefulness of bird populations (and changes in them) as monitors or indicators of how well we are doing in maintaining a diversity of natural biological communities. This is a conceptual reversal, in which we say not that the land manager has to have all that information in order to make wise management decisions, but that we may look to those bird populations (and changes in them) to provide useful feedback to the land manager as to the effects (on them) of his management programs.

Now this is a function that birds have been performing for man for centuries. Perhaps the prime example is the use of the canary carried in an open cage by the miner, which functioned as an efficient early warning system for the presence of mine gases and lack of oxygen (anoxia).

In more recent times a similar function has been performed by the birds of prey and certain other species, particularly the fish-eating birds, that feed at high trophic levels in long food chains. It is no accident that we have been forced to devote so much attention to studies of the raptors in recent years, no accident that the first indications of the effects of the organochlorine insecticides and related long-lived, fat-soluble compounds were found in the larger birds of prey such as the Bald Eagle *Haliaeetus leucocephalus*, Osprey *Pandion haliaetus* and Peregrine Falcon *Falco peregrinus*. In each case it was the position of the species at the apex of a long food chain that gave the species its usefulness as a monitor of contamination in that food chain. I suspect that the same phenomenon can be cited to explain the relative differences we are now observing in other raptor populations, e.g., that it is probable that differences in the distribution and abundance of the Cooper's Hawk *Accipiter cooperii* as compared to the Sharp-shinned Hawk *Accipiter striatus* and the Red-shouldered Hawk *Buteo lineatus* as compared to the Broad-winged Hawk *Buteo platypterus* can be related to the size and type of prey species commonly taken by each of those raptors.

Similarly, it is partly because of their fish diet that so much attention has been devoted in recent years to the herons, egrets and ibis, the long-legged wading birds that have been doubly affected by the loss of wetland habitats and their tendency to accumulate toxins by virtue of feeding in aquatic ecosystems, and even more recently, to the gulls and terns, the short-legged wading birds that similarly serve as excellent indicators of contaminated food chains.

It might be helpful at this juncture to look at the reasons why birds are particularly useful monitors of environmental contaminants and, as I have suggested, also may serve as monitors of the diversity of natural biological communities. The class Aves has many special characteristics, including numerous adaptations necessary for flight and for specialization in feeding, but those of concern here might include the following: 2/

2/ In developing this list of those avian characteristics that make birds especially useful as monitors of environmental contaminants and the diversity of natural biological

1. Birds are conspicuous, by virtue of the fact that they are largely diurnal, for most part live above ground, and must spend a considerable portion of the daily cycle in search of food.

2. The wide range of variation in bird size, the shape of the bill, neck, wings, legs and feet, and color variation in the plumage (reflecting the fact that like man and the primates they possess color vision) permits trained observers to identify many species in the field without having to resort to collecting.

3. Many species maintain territories, which further facilitates censusing them in the field, and particularly so in the case of the songbirds where the male sings to establish and defend his territory.

4. Birds are widely distributed through nearly all known habitats; as a class the Aves have a wider distribution than any other class of terrestrial vertebrates.

5. Birds are highly mobile, which means that their populations may rather quickly respond to perturbations in their food supply or to alterations in their habitats.

6. Many bird species are migratory and store fat before migration or in preparation for winter, thus accumulating stores of lipophilic (fat-loving) toxicants, which may have a delayed effect on mortality and hence be masked by displacement in the time and place of death because they are not mobilized until the fat is burned during migration or during a period of physiological stress.

7. Birds, like men, are warm-blooded, maintaining high internal body temperatures that in turn require maintenance of high metabolic rates; this means that birds must consume large quantities of highly nutritious protein-rich foods and hence may serve as high-volume food samplers.

8. In part to meet the demands of flight, birds have an efficient external respiratory system that is designed to handle large volumes of air; thus they may also serve as high-volume air samplers.

9. Some species absorb toxicants directly through their feet and hence may be susceptible to any airborne or air-deposited toxicants that may accumulate where they perch or walk.

10. Finally, more is known about the taxonomy of birds and more work has been done on their reproductive biology, life histories, behavior and physiology than has been done for almost any other class of terrestrial vertebrate.

It should be obvious that many of the characteristics that have made birds so useful as monitors of environmental contaminants may also make birds useful as indicators of change in forest ecosystems and as monitors of diversity in natural biological communities.

A further corollary of those characteristics is that they give us the capability of censusing bird populations rapidly, perhaps more rapidly than we can census other animal populations. The techniques by which we may census bird populations in forest ecosystems have already been established, and we can draw upon several existing data banks to establish baselines and to make the other comparisons necessary to interpret what is happening to bird populations in forest communities. These include the annual Breeding Bird Survey conducted by the U.S. Fish and Wildlife Service and the Breeding Bird Census and Winter Bird Population Study organized by the National Audubon Society and published annually in American Birds. Although the Breeding Bird Survey may be somewhat skewed toward edge-inhabiting species because of its dependence on roads, the Breeding Bird Census and Winter Bird Population Study constitute long-term data acquisition programs that offer a wealth of information as to the particular habitat requirements of many of the avian species that inhabit the northeastern and north central forests, and when these data are combined with what we already know of the life histories of nearly all North American birds, we have the basis for interpretation of responses of bird populations over the past 30 to 40 years to habitat alterations resulting from succession, logging, fire, windstorm, flooding, etc. Given these sources of information, which we can draw upon for both guidance and comparison, we should be able to determine which are the most useful indicator species for each forest community. I suspect that several of the papers to be presented at this symposium will identify key indicator species for various forest communities.

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communities, I drew heavily on an unpublished working paper, "Terrestrial vertebrate animals as biological monitors of pollution," prepared by Robert A. Lewis and Carolyn W. Lewis, Office of the Assistant Secretary for Environment, U.S. Department of Energy, Washington, D.C., as a contribution to the International Workshop on Monitoring Environmental Materials and Specimen Banking, Berlin, German Federal Republic, October 1978.

RELATION TO ECOSYSTEM MANAGEMENT

Earlier in this paper I suggested that we attempt to change our thinking, to make a conceptual reversal and focus not on how difficult it is to manage diverse habitats for nongame birds but rather to look to the bird populations themselves (and changes in them) to provide feedback as to how well or how poorly we are doing in managing forest habitats.

I also think that we need to recognize the implications of an attempt to manage forest communities for nongame birds, which is that, in order to accomplish this task without favoring one species or group of species at the expense of another, we must abandon single-species management and move toward ecosystem management.

To some extent this need to reorient our programs toward ecosystem management has been masked by other management directives that have come down the pike in recent years, most notably the requirements of the Endangered Species Act of 1973 and subsequent amendments. Just as many of us in the environmental and conservation communities were becoming aware that we could no longer practice single-species management to favor gamebirds and game animals without affecting nongame species, our attention was drawn to the need to devise special programs, based on single-species management, for endangered and threatened species. This is clearly required by the Endangered Species Act, as amended, in that any federal program or federally funded or permitted program is required by law to take into account the needs of endangered species and, in the case of federal land management agencies, to manage for them. But even this program of single-species management, however necessary, may now be approaching the point of diminishing returns as more and more endangered species are identified and listed. We have the capability for developing single-species management programs for a limited number of endangered or threatened species that occur in forest communities, but we may soon reach the point where what is necessary for one endangered species may conflict with what has to be done for another. Clearly, that point has already been reached in the Hawaiian forests, where the individual requirements of an entire assemblage of forest-dwelling endemic Hawaiian birds, all endangered, can only be met by attempting to manage the Hawaiian forest ecosystem as a unit, rather than attempting to devise separate single-species management programs for each of the endangered Hawaiian forest birds. I suspect that as we continue to develop the Endangered Species Program in North America and extend it to the flora as well as the fauna, it will become necessary to reorient that program more and more toward full ecosystem management.

There are certain other exceptions to the ecosystem management approach that spring to mind, most notably the need for special programs to meet the requirements of the birds of prey, special attention to meeting the requirements of cavity-nesting species in our forests, a high priority for the preservation of wetlands in our forest communities, and the need for special programs to deal with introduced or exotic species. Yet, if we are going to manage forest communities for nongame birds, we must, on the whole, reorient our programs from single-species management of our forests to an ecosystem approach, managing the forests for the benefit of all of their inhabitants and favoring no one group to the exclusion of another.

As my final point in this paper, I want to suggest that the only way in which we may successfully manage forest ecosystems for the benefit of nongame birds and all of their other inhabitants is to set as the principal objective of management for nongame species the maintenance of a high degree of diversity in natural biological communities. Let us return to that common theme that ran through so many of the papers at the Tucson symposium. If we accept the fact, as I believe we must, that we do, indeed, lack knowledge of all the interconnections (all of those interactive pathways of trophic web organization), we may be led to a very different conclusion: -----not that we cannot, for lack of that knowledge, manage forest communities for the benefit of nongame species, -----but that, precisely because of that lack of knowledge of all of those interconnections, we must manage for diversity, must do our best to preserve all of the elements of our forest ecosystems because we do not know enough to pick and choose among them. This is a cautious and profoundly conservative position, but it is supported by a considerable body of hypotheses and reasoning that, on the whole, suggests that diversity of natural biological communities may be our best protection against man-induced or natural perturbations of those ecosystems (Dearden 1978). This is drawn from the hypothesis----it is only a hypothesis but it is one that I find convincing---that the more diverse system, as contrasted to the less diverse system, has a greater capacity for self-restoration, precisely because it has a greater number of interconnections, interactive pathways, one or more of which may serve as the regulating and restoring mechanism.

If we take the maintenance of a high degree of diversity of natural biological communities as the principal objective of our management program for nongame birds, then the importance of birds in forest communities, to the manager, may well be that function outlined in this paper, that of supplying the feedback that the manager requires as an indication of just how well or how poorly his management programs are doing in meeting that objective.

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HABITAT STRUCTURE, SUCCESSION AND BIRD COMMUNITIES

Stanley H. Anderson[1]

Abstract.--Birds select habitats by several different mechanisms to supply the requisite needs of the species. Several statistical tests can be used to correlate bird species with habitat variables. Combining variables by means of factor analysis can indicate how species relate to forms of disturbance in forest habitats.

Natural changes in forest community structure that occur in plant succession can be altered by many human caused disturbances. These disturbances, which include fire, logging, increasing edge, retention of snags and maintaining a diverse habitat, are also effective tools for the manager of nongame birds.

INTRODUCTION

If you are a bird watcher you know that different species of birds are found in characteristic habitats. To find Barred Owls[2], for example, you go to hardwood forests in wet or swampy riverbottoms at night. The Black-backed Three-toed Woodpecker is found deep in coniferous forests where fire, logging or wind have left some standing snags with heavy understory. The Great Crested Flycatcher is often found in large woodlands with small openings and perch sites. The Red-breasted Nuthatch is wide ranging in mature evergreen forests whereas the White-eyed Vireo can be seen in the shrub and understory of southern forests and forest edge. The Black-and-white Warbler is found in mature forests and the Swamp Sparrow nests in bogs and marshes.

In North America there are 821 species of birds of which at least 225 species occur in the regions of concern to members of this Workshop. How can we manage for that large a number of species with their diverse needs? The key is to understand why species are found in a particular habitat, how habitat changes affect them, and how to manage for assemblages or communities of birds rather than individual species.

AVIAN HABITAT SELECTION

Why are birds where they are? Birds adapt to areas where their requisite needs are found. Their breeding habitat must supply all the needs, including nesting site, nesting material, food, and protection for each species. Within the evolutionary process, birds develop mechanisms enabling them to find these areas. When they arrive in their habitat they apparently instinctively perceive signals from the environment indicating their requisite needs are present (Klopfer and Hailman 1965, Wiens 1969) and do not attempt to breed in other habitats (Lack 1933). Some species of birds are known to imprint on the place of their birth. For example, Klopfer (1963) shows how Chipping Sparrows return either to the deciduous or coniferous forested areas around North Carolina depending on the particular forest in which they are born. Hilden (1965) summarizes several studies on gulls to show learning in habitat selection.

Since territorial animals seek their habitat rather than randomly disperse and settle through the environment, ethologists feel that structural features of the habitat provide "sign stimuli" (Lack 1933, 1937, Hilden 1965). These stimuli serve as forms or guideposts to indicate which habitats can be expected to supply the species' needs (Wiens 1969). It is most important to recognize that minor habitat alterations which destroy such "sign stimuli" can result in changes in bird species composition. Although a species might be found in a number of habitat types, the population in each habitat has characteristics that separate it from another. For example, when morphological characteristics of Red-breasted Nuthatches are examined in western Oregon, different bill and leg sizes are found in the fir and pine populations (Fig. 1) (Anderson 1976).

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[2] See Appendix 1 for scientific names of bird species discussed in paper.

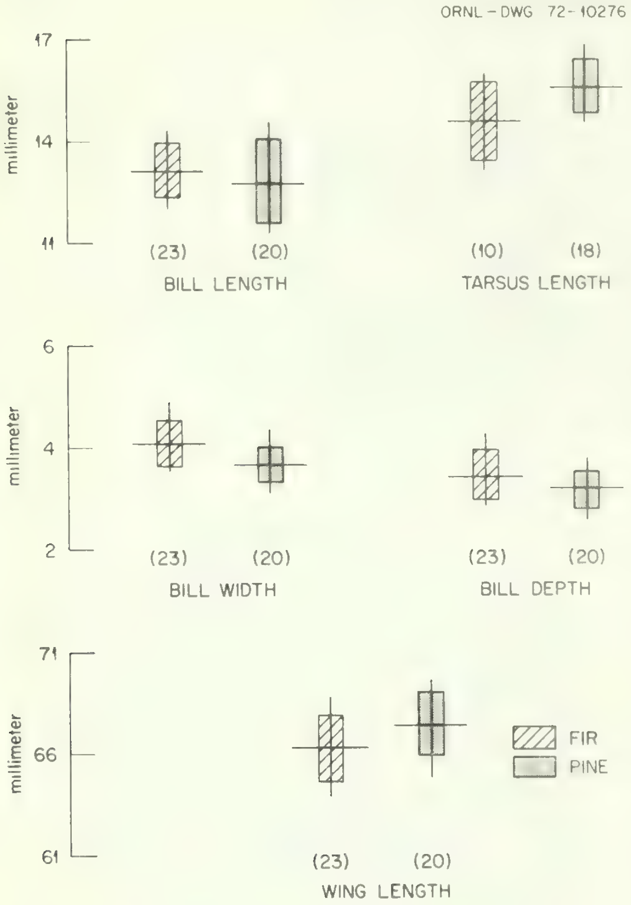

Figure 1.--Selected morphological characteristics of Red-breasted Nuthatches in western Oregon fir and pine forests. A two-tailed t-test shows a significant difference betwee the bill width, depth, and tarsus length. Horizontal line is the mean, rectangle represents the standard error, and vertical line the range.

Whereas most species seem to respond to the structure of the vegetation, other visual clues provide information about the habitat. Svardson (1949) indicates that water, overlooks, vegetation on the ground, and the shade of green influence the areas selected by some species of English birds.

Migratory birds do not begin to establish their territories or select nest sites until some weeks after they arrive in breeding habitat (Tinbergen 1961). Once birds have established their territory, they remain fixed to these sites despite frequent adverse conditions. Emlen (1970) shows that bird counts in Florida pine stands are essentially the same in burned and unburned stands when fire burned the area during the breeding period.

Habitat structure, however, is the basic reason for the presence of birds in an area. Management of nongame birds, therefore, requires an understanding of the habitat structure and avian response mechanisms.

HABITAT CORRELATION

Information on the habitat of nongame birds can best be used by wildlife managers if it is translated into measurable features. Research biologists began to quantify habitat variables and correlate them with bird species in the late 1950s and 1960s. While more needs to be done on this subject, particularly in terms of seasonal and latitudinal differences, there are results that can be used by managers.

To describe avian habitat in Arkansas, James (1971) uses multivariate methods to indicate differences in vegetation variables. She points out that each species has a perceptual world to which it responds as an organized whole (niche-gestalt). This technique allows biologists to quantify the different vegetation components necessary for the species. Warbling Vireos are found in deciduous forests 40-100 feet tall that are relatively uniform in height and near the edge habitat. White-eyed Vireos show a preference for forests with mixed size class trees around 40 feet tall. Specific components can be listed for each bird species in the forest (Fig. 2).

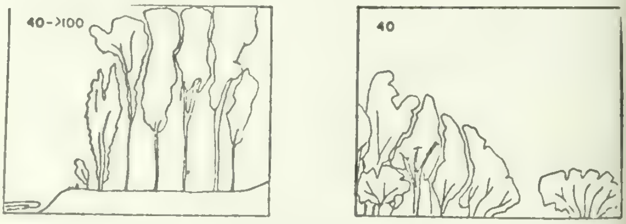

Figure 2.--Outline drawings of the niche-gestalt for the Warbling Vireo (left) and the White-eyed Vireo (right). Numbers give vertical scale in feet (from James 1971).

In another study using multivariate analysis, Anderson and Shugart (1974) show that Downy Woodpeckers in an east Tennessee deciduous forest are correlated with the number of saplings. White-breasted Nuthatches are correlated with understory vegetation and the biomass of trees in the lowest woody vegetation layer (Fig. 3). White-breasted Nuthatches

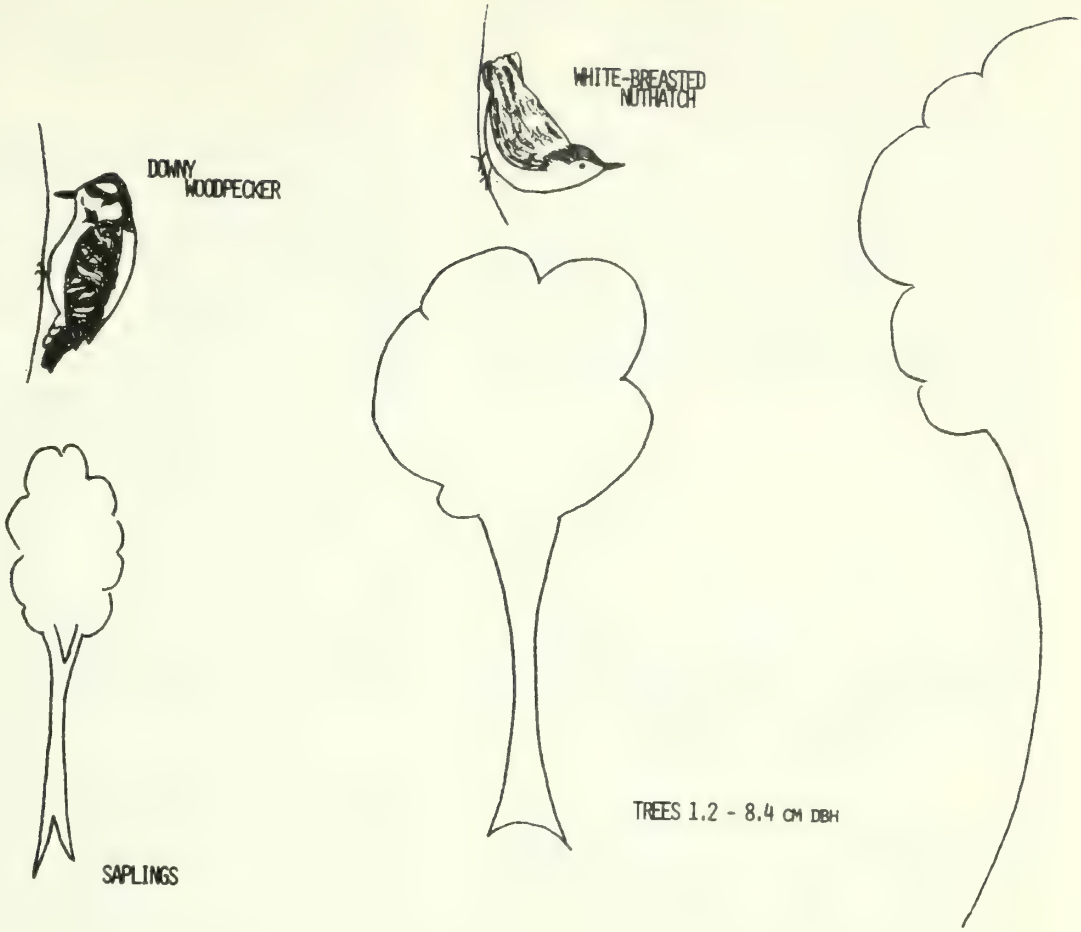

Figure 3.--Trees associated with Downy Woodpecker and White-breasted Nuthatch in east Tennessee deciduous forest (from Anderson and Shugart 1974).

and Downy Woodpeckers thus select their habitat using similar criteria. The distinction is that the woodpecker is found in areas with well developed understory whereas the nuthatch is in areas of sparse understory.

Whitmore (1975) used discriminant function analysis to determine important habitat variables for bird communities in Utah. He found that the percentage canopy cover was the most important individual habitat characteristic that could be used as a predictor of which bird species occupy a particular environment. The shrub density, number of trees 7.5 - 15 cm DBH and percentage ground cover followed in order of priority.

Ordination by means of principal component analysis is also possible as demonstrated by Smith (1977) in Arkansas. There he uses a combination of all habitat data to form the principal component axis. He found an ordination of birds along this axis with most species concentrated toward the moist forest.

Factor analysis is another statistical technique that is very similar to principal component analysis. Each test reduces the habitat variables in a multidimensional space to a linear component. Principal component analysis scales the variables so that the sum of the squares for the element in each vector equals one. When this is done the associated eigenvalue (characteristic root) is interpreted as the variance along the principal component axis. Vectors in factor analysis are scaled so that the coefficients are the correlation coefficients with the original measurements.

Factor analysis was used to evaluate the habitat of breeding birds in the Upper

Peninsula of Michigan. The purpose of this study was to evaluate the effect of a wildfire that burned over 260 square kilometers on the Seney National Wildlife Refuge in 1976. Seven paired eight-hectare plots, one of each pair on burned and one on unburned habitat, were established to conduct the evaluation. Two major habitats, the northern mixed forest and the bog/fen, were burned on the Refuge. The mixed forest consisted of a few pure stands of black spruce (*Picea mariana*), paper birch (*Betula papyrifera*) and quaking aspen *(Populus tremuloides*). There were many areas where the forest was quite open and trees sparse, allowing dense concentrations of alder to grow. Most of the region consisted of a mixture of aspen, cherry, spruce, maple, pine, fir and birch.

The fire burned in a very erratic manner. In some places it destroyed virtually all of the standing timber. In other places the fire simply burned in and around the bottom of trees, destroying some of them. In the spring following the fire, seedlings of quaking aspen and jack pine (*Pinus banksiana*) as well as lowbush blueberry (*Vaccinium augustifolium*) and bracken fern (*Pteridium aquilinum*) grew on the burned ground. By the spring of 1978, two years after the fire, the ground had a rich cover of aspen seedlings and blueberry.

On the Seney Wildlife Refuge, the bog habitat was covered by a thick layer of peat resting on sandy soil. The area had long (up to 2 kilometers) dense bog forests that were less than 0.25 kilometers wide. Tamarack (*Larix laricina*) and red maple (*Acer rubrum*) were the common tree species. Between the forests were flat bogs containing typical bog plant species as well as short tamarack and bog birch (*Betula pumila*). Fire burned rapidly through some of these areas, destroying the trees, grasses, sedges, and the upper layers of peat. Interspersed in the open bog areas were small sand islands less than 0.04 hectares with populations of red and white pine or aspen and birch. Most of the sand islands were no larger than a hectare.

Each plot was censused for breeding birds eight times each spring in 1977 and 1978. All birds heard and seen were recorded. The vegetation data were collected on ten 0.04-hectare points randomly selected within the plots by means of a modified James and Shugart (1970) method.

An ordination of the plots (Figs. 4, 5) was constructed by a principal axis factor analysis of the habitat variables with a varimax rotation (Overall and Klett 1972, Greg-Smith 1964, and Barr *et al.* 1976). Unrotated principal axis factors only differed for principal components by a scaling factor. Varimax rotation was used to obtain a simple structure that was easier to interpret. The factor scores for the variables on Table 1 allow the selection of the most significant variables.

An examination of the loading of the first factor shows that it represents the mature forest, with a strong positive correlation to the number of trees, the percentage canopy closure, and the mean canopy depth (high values for this variable indicate the presence of conifers). The second factor represents the effect of the burn and has a high positive correlation with the number of snags and the number of seedlings. The most marked change on burned plots between the first and second growing seasons after the fire is the high number of seedlings, mainly aspen (*Populus tremuloides* and *grandidentata*), that become established on the charred soil. High numbers of seedlings on unburned plots are due to advanced reproduction. The third factor represents the shrub component of the vegetation. The factor scores for variables on each plot can be examined (Table 2) and compared with the composite scores (Table 1) to determine the variation of the plot from the mean.

Figure 4 shows the two dimensional ordination of plots in the space of the habitat factors. The burned and unburned plots are best separated on the basis of factors one and two. All unburned plots except 6 and 7, which are located in the relatively open bog/fen, have positive scores for Factor 1. Burned plots 6 and 7 likewise have negative values for Factor 2. The dead trees of plot 6 are not standing as snags because the supporting root systems are burned away. The burn on plot 7 is not severe and has little effect on the bog shrubs and the few small trees. When Factor 3 is added (Fig. 5), burned and unburned plots 6 are clearly separated. There are high numbers of bog and lowland shrubs on the unburned plot of the pair; however, recovery cannot occur quickly because the shrubs and top layers of peat are burned away. Two years after the fire, only sedges (*Carex* sp.) and cotton grass (*Eriophorum* sp.) are established.

Burned plot 4 stands out as having scores close to zero for all factors. A smaller (72%) portion of this plot burned with a less intense fire. Consequently fewer trees are dead. The living trees give this plot a higher percentage of canopy closure than several of the unburned plots.

The factor score for each bird species is determined on the basis of weighted variables of the plots where the species is found (Table 3). Selected bird species are added

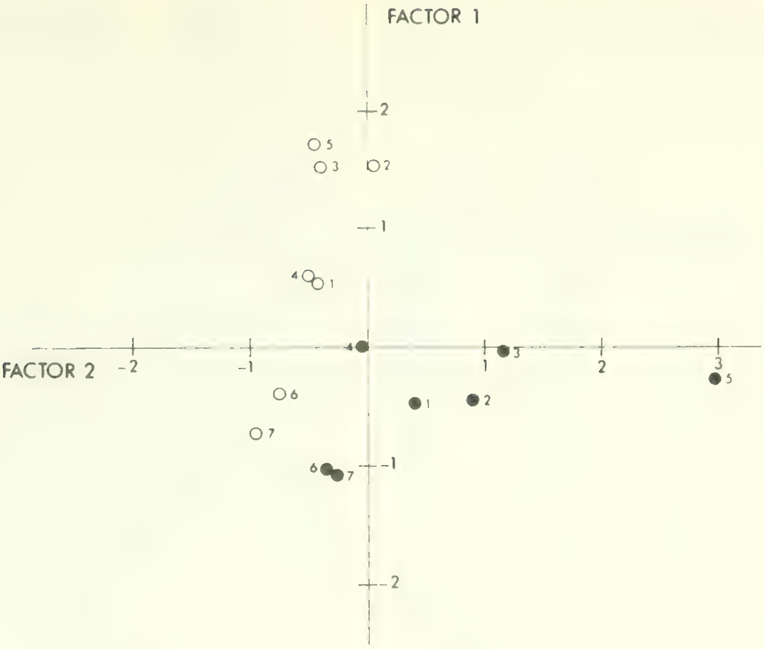

Figure 4.--Ordination of 20-acre plots on Seney National Wildlife Refuge in space of habitat factors 1 and 2 formed by a principal axis factor analysis with a varimax rotation. Dark circles represent burned plots, light circles represent unburned plots.

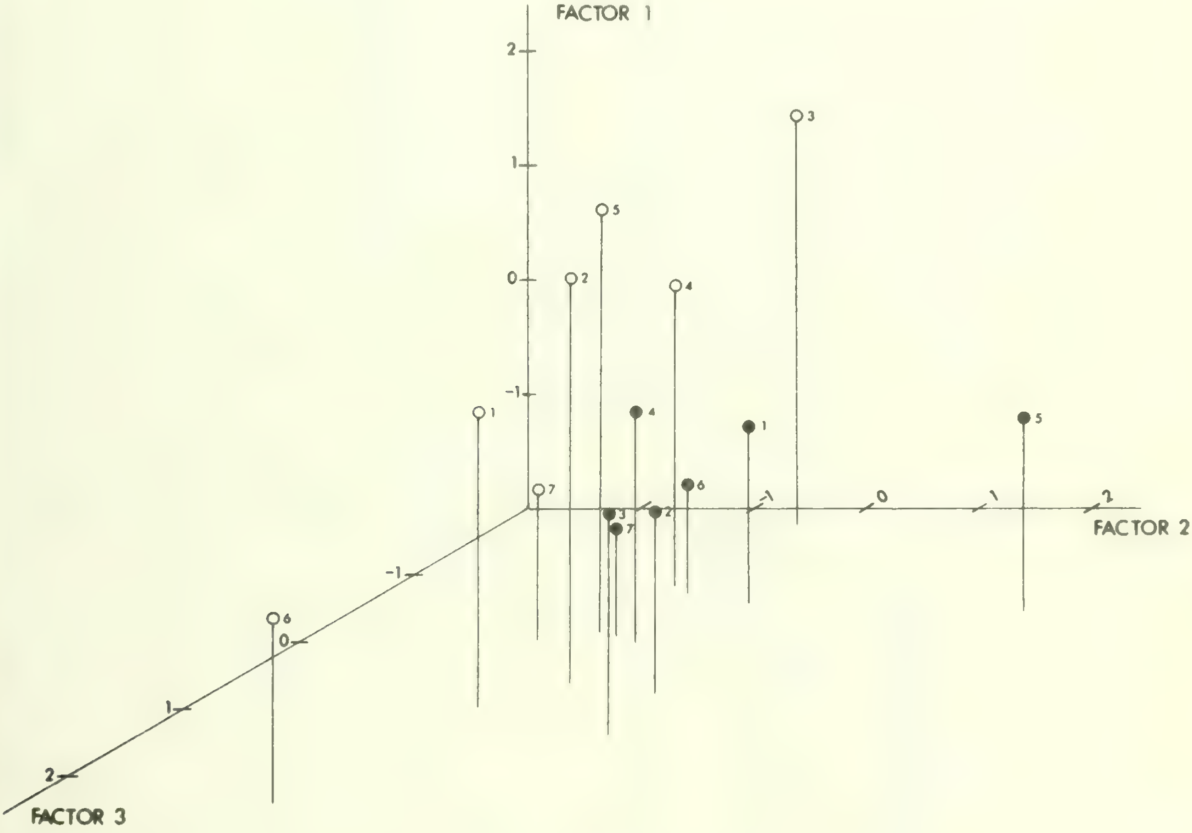

Figure 5.--Ordination of Seney plots as discussed in Figure 4 in space of factors 1, 2 and 3.

Table 1.--Habitat factor loadings (correlations with observed habitat variables) for the principal axis factor analysis with a varimax rotation.

	Factor 1	Factor 2	Factor 3
Trees 24-44 cm DBH	0.7367	-0.0107	-0.3713
Trees < 24 cm DBH	0.8180	-0.0780	-0.1465
Shrubs 50-150 cm tall	-0.1730	-0.0656	0.8408
No. saplings	0.5732	0.0928	0.6400
No. seedlings	0.0042	0.8564	0.1288
No. snags	-0.0312	0.8751	-0.1400
% of plot burned	-0.6004	0.5534	-0.1087
% canopy closure	0.9521	-0.0403	0.0148
Mean canopy depth (meters)	0.9417	0.1408	-0.0795
% cover - grasses and sedges	-0.5936	-0.6002	-0.0170

to Figure 6 by using the weighted variables. Species such as the Savannah Sparrow found only on burned plot 6 have the same factor scores as that plot. Bird species found on several plots are clustered in the center of the figure. The Black-backed Three-toed Woodpecker, strongly influenced by the presence of conifer snags, is located far to the right on the figure, with a high positive score for Factor 2. Species using plots with high numbers of trees (e.g., Cape May Warbler and Ovenbird) have a high positive correlation with Factor 1, represented by the vertical line supporting the species symbol on the figure.

Management for nongame birds can be most effective when the key habitat components associated with each community are known. While a number of biologists show that an increase in the structural complexity of a community is associated with an increase in bird species (MacArthur and MacArthur 1961; MacArthur, *et al.* 1966; Karr 1968), the effect of habitat change must be evaluated in terms of individual or groups of habitat components.

PLANT SUCCESSION AND BIRDS

Plant succession occurs, according to McIntosh (1970), because most species are temporary occupants of a site. Plants tend

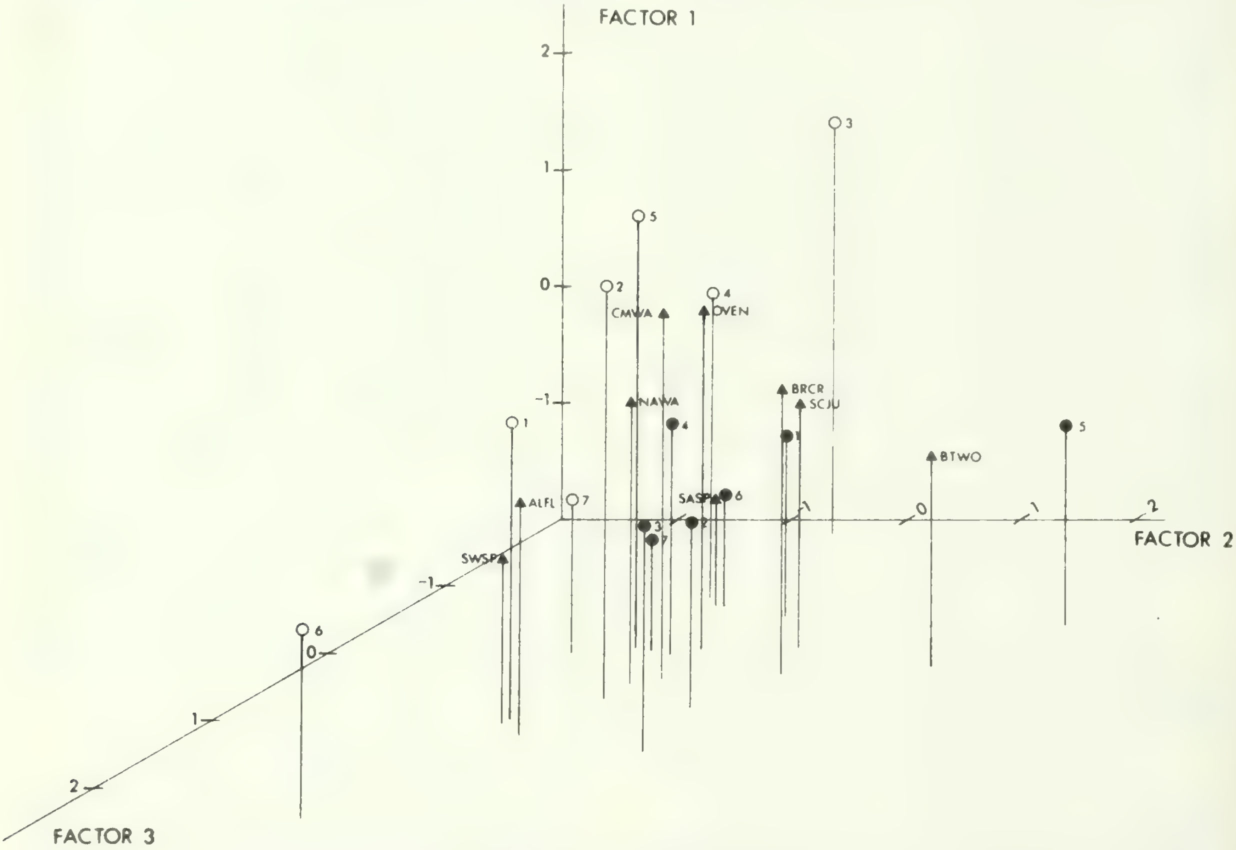

Figure 6.--Ordination of Seney plots in Figure 5 and selected species of birds. Species code in Table 3.

Table 2.--Factor scores and observed habitat variables for plots.

				UNBURNED			
	Plot number 1	2	3	4	5	6	7
Factor 1	0.52	1.53	1.52	0.64	1.74	-0.37	-0.73
Factor 2	-0.43	0.05	-0.41	-0.52	-0.42	-0.77	-0.90
Factor 3	0.97	0.66	-1.76	-0.77	-0.12	2.46	-0.01
Trees 24 - 44 cm DBH	6.00	16.00	65.00	13.00	15.00	0.00	0.00
Trees < 24 cm DBH	183.00	364.00	113.00	167.00	604.00	124.00	4.00
Shrubs 50 - 150 cm tall	1928.00	808.00	48.00	224.00	728.00	7224.00	1504.00
No. saplings	68.00	72.00	20.00	16.00	32.00	32.00	16.00
No. seedlings	1040.00	6400.00	160.00	80.00	40.00	80.00	240.00
No. snags	25.00	25.00	19.00	11.00	32.00	19.00	0.00
% of plot burned	0.00	0.00	0.00	0.00	0.00	0.00	0.00
% canopy closure	24.50	70.50	45.00	31.00	59.00	17.20	0.20
Mean canopy depth (meters)	6.23	7.38	10.06	7.83	9.55	2.36	0.86
% cover - grasses & sedges	22.50	11.80	3.00	11.20	2.10	33.20	40.00

				BURNED			
	Plot number 1	2	3	4	5	6	7
Factor 1	-0.49	-0.42	-0.01	0.01	-0.26	-1.07	-1.10
Factor 2	0.38	0.87	1.16	-0.09	2.95	-0.32	-0.28
Factor 3	-0.61	0.81	1.45	0.05	-0.42	-0.73	-0.08
Trees 24 - 44 cm DBH	3.00	2.00	9.00	12.00	9.00	0.00	0.00
Trees < 24 cm DBH	39.00	45.00	54.00	97.00	87.00	3.00	2.00
Shrubs 50 - 150 cm tall	736.00	1744.00	3472.00	2808.00	1240.00	624.00	2352.00
No. saplings	8.00	56.00	72.00	12.00	4.00	0.00	0.00
No. seedlings	2960.00	8040.00	6200.00	680.00	18720.00	320.00	0.00
No. snags	53.00	52.00	112.00	39.00	360.00	4.00	0.00
% of plot burned	100.00	94.50	100.00	72.00	79.50	100.00	100.00
% canopy closure	13.50	7.50	9.20	29.30	16.50	0.50	0.20
Mean canopy depth (meters)	3.77	2.55	6.28	6.04	4.56	0.60	0.44
% cover - grasses & sedges	12.60	10.70	3.10	18.70	2.20	33.80	26.40

Table 3.--Factor scores for bird species.

Species (code)	Factor 1	Factor 2	Factor 3	Number territories
Alder Flycatcher (ALFL)	0.0931	-0.1498	1.2255	7.5
Brown Creeper (BRCR)	0.4900	1.2293	0.3025	3.0
Black-backed Three-toed Woodpecker (BTWO)	-0.1769	2.3538	0.2003	1.5
Cape May Warbler (CMWA)	1.1510	0.1942	0.3266	22.0
Nashville Warbler (NAWA)	0.4335	0.0274	0.4434	39.0
Ovenbird (OVEN)	0.8609	0.1386	-0.0883	33.0
Savannah Sparrow (SASP)	-1.0686	-0.3196	-0.7346	3.0
Slate-colored Junco (SCJU)	0.1510	1.0649	-0.0884	13.0
Swamp Sparrow (SWSP)	-0.3254	-0.4421	1.0933	9.5

to invade an area when the resident species change the habitat so the residents cannot effectively compete with invaders. Actual stages of plant succession might or might not coincide with distinct bird communities as birds respond to structure.

In a study in the Algonquin Provincial Park in Ontario, Martin (1960) reported that birds occurred when their niche requirements were satisfied. Martin pointed out that you could list a group of birds for each forest type in the park, but most species overlapped into several plant community associations. He also showed that bird species were found in different vertical strata in the different plant communities.

On the Apostle Islands of Wisconsin, distinctive patterns of hemlock, pine, aspen, red oak, sugar maple, and percentage of understory contribute to the bird species diversity (Beals 1960). The lack of pattern for spruce and fir could reflect the important difference of associated tree species according to Beals. This lack of pattern is particularly true of the northeastern and north central forests. Kendeigh's 1948 study on the northern lower peninsula of Michigan shows that plant communities there have a very non-uniform structure. In that study, aspen--red maple forests contain two bird communities and red pine--aspen, a mingling of three bird communities. This information, he points out, is an indication that bird species do not directly recognize the same seral stages as plant communities.

Most workers find that avian species and diversity increase through progressive successional communities toward climax vegetation (Johnson and Odum 1956, Shugart and James 1973). These results are similar in both deciduous and coniferous forests. Karr (1968) notes a slight decline in bird species and in density in late forest stages. Bond (1957) used a vegetation continuum index devised by Curtis and McIntosh (1951) to correlate populations of breeding birds to tree species composition. This study in southern Wisconsin has obvious relationships to community succession. It also shows how bird species and diversities change in different stages of succession.

Logging and fire are two forms of habitat destruction to which succession can be related. Fire historically serves as an important factor in the regeneration of forests of the north central region. Following fire an area generally reverts to an early stage in succession. Adams (1908) shows the importance of fire in maintaining open areas on Isle Royale, Michigan. Niemi (1978) shows that bird species, especially small passerines, decrease following fire in northern Minnesota. The study at the Seney National Refuge indicates that some bird species are attracted to burned areas and others leave the disturbed areas (Table 4).

Table 4.--Bird species on Seney National Wildlife Refuge significantly affected by the 1976 fire.

Increased following fire:
- Eastern Kingbird
- Brown Creeper
- Cedar Waxwing
- White-throated Sparrow
- Song Sparrow

Decreased following fire:
- Veery
- Black-and-white Warbler
- Magnolia Warbler
- Cape May Warbler
- Chestnut-sided Warbler

These data, developed by means of an analysis of variance test, show that 10 species of birds are affected by the fire. In addition, in the mixed forest the Alder Flycatcher, Black-throated Green Warbler and Nashville Warbler are common in the unburned area, while the Yellow-rumped Warbler, American Robin, Lincoln's Sparrow, Killdeer and Black-backed Three-toed Woodpecker are observed most frequently in the burned forest.

The bog forest has American Redstart, Black-and-white Warbler, Canada Warbler, Nashville Warbler and Swamp Sparrow, which are not found in the burned bog area. The only species found in the burned bog area and not in the unburned area are Savannah Sparrow and Brewer's Blackbird.

Birds moving into burned areas are probably attracted by features such as snags which attract woodpeckers and bark-foraging species and perches for insect hawking species. Succession following a fire can increase the diversity of birds as the shrub layer thickens below the burned snags, and seedlings and shrubs develop rapidly in the area. Heinselman (1973) stated that the entire biota of the Boundary Waters Canoe Area of Minnesota are adapted to periodic fire. Succession resulting from fire restructures the entire system.

Bird species diversity on the Seney Refuge was higher on the burned plots than on the unburned plots. Species such as the Black-backed Three-toed Woodpecker, Brown Creeper and Slate-colored Junco, which were uncommon in burned areas, were found in the burned habitat. Very few species were found exclusively in the unburned habitat although the populations found in dense forests were lower than in the burned habitat.

Clearcutting, on the other hand, destroys segments of the forest creating open areas with much debris on the ground. When whole forests are destroyed, as occurred in northern Minnesota and Wisconsin in the early part of the century, the avian community changes.

In a study on five stands of northern hardwood forest in the Adirondack Mountains of northeastern New York, breeding bird census sites were established to verify the effect of logging. None of the bird species were eliminated by logging, but some were recorded only in logged stands (Webb *et al.* 1977). They found that in this 10-year study the number of species and the species diversity index increased in the logged areas and were correlated positively with logging. Hagar (1960), in a study of Douglas fir (*Pseudotsuga taxifolia*) in California, found that little change occurred in the number of species immediately following logging. He indicated that a change occurred in the species composition 3 years following logging.

Natural succession should be considered in nongame bird management. Total diversity can be maintained at a higher level when forests consist of different successional seres. Habitat change can be planned around the forest succession sequences and the nongame bird communities.

MEASUREMENT OF CHANGE IN BIRD COMMUNITIES

It is important to be able to measure the changes in bird communities as they occur in a forest.

Diversity. A bird species diversity index (BSD) can be one means of measuring change. Diversity is measured by counting the number of individuals and the number of species, then noting the distribution of individuals among the species. Thus communities with low BSDs tend to have large numbers of birds in one or a few species and very few individuals in other species. Communities with high BSD have a more or less uniform distribution of individuals in all species. To use diversity indices it is important to have comparative figures. Thus the BSD of different successional seres might be compared. Diversity before and after disturbance can be used. MacArthur and MacArthur (1961) show how BSD increases with the diversity of the vegetation in the three different layers (foliage height diversity - FHD) they use. Habitats with more uniform distributions of tree, shrub and ground layers contain higher bird species diversities. Willson (1974) cautions about using such indicators after finding a lack of correlation between BSD and FHD.

Wildlife managers, however, can use the diversity concept to maintain nongame bird communities. By measuring BSD in a forest and maintaining important habitat factors correlated with key species, it is possible to maintain diverse communities. Habitat diversity is an approach that can be contrasted with single species management of game or endangered species.

Care should be taken in using the diversity techniques as all bird species contribute to the diversity. Thus, some less desirable species, such as Starlings and House Sparrows, or highly adaptable species such as Gray Catbirds and Cardinals, are able to substitute for some of the more specialized species of forest birds. Studies should be made on carefully delineated communities. The clue is to establish a habitat for the bird community desired and use diversity as one of the tools of measurement.

Indicator Species. Species that characterize a community are indicator species. While it is difficult to define this term because there are so many species in a community, it is possible to identify major bird assemblages with each successional sere. The changes that occur as succession proceeds in a forest make it possible for us to look at different birds that are found in different community types. Bird species frequently overlap between two plant seres so bird communities do not always coincide with plant communities. However, by managing for the selected bird species found in each seral stage we can attract an entire community. We must still be sure that minor or endangered populations are not lost because of our effort. It is important to realize that management for indicator species means managing for the whole community. It is also possible to use one of the lesser or endangered populations as an indicator.

Data from the Seney National Wildlife Refuge and data from Martin's (1960) study in Ontario, Canada, are used to show key indicator species in bog, boreal forest and deciduous forest communities (Table 5).

NONGAME BIRD MANAGEMENT IN THE NORTH CENTRAL FORESTS

Managers have a number of techniques available to them for managing nongame communities.

Table 5.--Common birds of bog, boreal forest and deciduous forest in north central United States (source, Martin 1960 and Anderson unpublished data).

Bog	Boreal Forest	Deciduous Forest
Eastern Kingbird	Spruce Grouse	Eastern Wood Pewee
Tree Swallow	Golden-crowned Kinglet	White-breasted Nuthatch
Common Yellowthroat	Ruby-crowned Kinglet	Wood Thrush
Red-winged Blackbird	Cedar Waxwing	Veery
Lincoln's Sparrow	Magnolia Warbler	Red-eyed Vireo
Swamp Sparrow	Myrtle Warbler	Ovenbird
Song Sparrow	Northern Waterthrush	Scarlet Tanager
	White-throated Sparrow	Rose-breasted Grosbeak

Fire. Much of the north central forest region was periodically affected by fire before white man. Fire largely determined the composition and structure of the presettlement vegetation in such areas as the Boundary Waters Canoe Area, the Upper Peninsula of Michigan, and a good portion of northern Wisconsin and Minnesota. These fires burned in irregular patterns throughout the area, opening up the understory, creating additional edge, and thereby creating habitat for many bird species.

Some species, such as the Kirtland's Warbler, are dependent on fire for periodically opening habitat. A number of other species, including Upland Sandpiper, Mourning Dove, Common Nighthawk, Common Flicker, Eastern Kingbird, Black-capped Chickadee, House Wren, Brown Thrasher, Eastern Bluebird, Nashville Warbler and Vesper Sparrow, are reported by Pinkowski (1977) to receive benefits from jack pine burns in Michigan. Studies by Heinselman (1973) and Niemi (1978) also demonstrate the effect of fire on birds in the north central region.

A small prescribed burn can be used to clear the understory or some of the ground litter and allow ferns and aspens to spring up to provide seed and other food for birds. Larger burns can be used to actually change the structural component of the vegetation. A very intense fire could destroy the entire forest and set the area back to the earliest stages of succession. Intense fires are much more common in the western United States.

Clearing Vegetation. Selective logging, clearing understory and removing small stands of timber all have major impacts on the avian community. They all serve to increase bird diversity in the north central forest. They attract edge species and provide a temporary mixture of both forest specialists and edge generalists. Flycatchers can hawk in the open area and woodpecker activities increase on the more exposed tree and snag branches. Clearing the understory allows some species to move into forested areas previously unavailable to them because of dense vegetation. This technique is particularly effective when the habitat requirements of bird communities are considered for each successional sere.

Edge. A number of studies have shown the value of edge to birds. Lay (1938) indicated that wildlife increased in a mixed Texas forest where small clearings were established. Hagar (1960) found that logging in a western Douglas fir forest increased the bird population density along the edge within 3 years after cutting. Johnson (1947) believed that the forest edge was a distinct community because it was inhabited by species that in part displayed adjustments to the particular niche available only in forest edge. Kendeigh (1946) documented the high species diversity in the deciduous-coniferous forest ecotone.

Managers can use the edge concept to maintain the diversity of the north central forest birds. Another paper in this Workshop addresses the dangers of introducing edge into forest interior situations and discusses the minimum edge-free area required to support different species of forest interior birds. This very important feature should be considered when deciding whether to manage avian communities by increasing edge. Increased edge can actually reduce the number of nongame species if the forest becomes fragmented into small isolated units.

Using these guidelines, one should consider edge between forest and field or edge created by human disturbances such as logging, transmission-line corridors and roadways. These cuts are continuing to increase the amount of edge and reduce the size of unbroken forested area. A study in an east Tennessee deciduous forest shows that transmission-line corridors reduce the area for nesting migratory bird species but increase the nesting potential for resident birds (Anderson in press). The additional open area brings in some gallinaceous birds, as well as the raptors and other predators, which can hunt along these transmission lines.

Snags. Snags or dead trees are considered undesirable by many land managers and are viewed with mixed emotions by wildlifers. We now are aware of some 85 species of North American birds that excavate nesting holes or use holes created by other species in dead or deteriorating trees (Scott *et al.* 1977). Since the majority of all cavity nesting birds are insectivorous, they play a valuable role in the forest ecosystem. Maintenance of snags does benefit hole-nesting species (Haapanen 1965).

The great majority of hole-nesting species are permanent residents or short distance migrants (owls, woodpeckers, chickadees, nuthatches, wrens and bluebirds). Another paper in this Workshop will address some problems associated with leaving snags standing throughout a forest.

Nest boxes can be substituted for snags to draw more cavity nesters or increase their nesting success. Game biologists attract wood ducks, mergansers and a few other species by properly placing nest boxes. Experiments with some species of chickadees show population increases when nest boxes are placed in wooded areas with insufficient nesting cavities. We need to conduct studies on the behavior of species using nesting boxes to determine how far apart they should be placed for maximum utilization.

Habitat Diversity. Very few areas have extensive uniform avian habitat; rather, small islands of forest are found around fields and forests are segmented by roadways and clearcuts. Succession can also vary due to slope, exposure, climate and historical use. Uniform forests such as those found on tree farms often have a lower bird species diversity than those with a mixed age class. Forests having a diversity of structure generally attract the largest bird diversity.

Planned Management. Effective management for nongame birds requires a plan based on desired goals and specific methods.

Once the area to be managed is selected and the purpose for management established, employable methods to fulfill that purpose must be chosen. One management possibility could involve allowing the area to proceed toward natural succession and climax--a policy of let nature take its course. The result is likely to be an increase in diversity and changes in the bird species much as would occur in a climax vegetation. The population or diversity of birds is highest in the near climax communities. If a large region is allowed to reach climax forest, total diversity and species composition will be reduced. Second, the area can be maintained for diversity by special techniques, such as clearcutting the understory, prescribed burns, or some profitable form of logging. Management of an area under these principles really is the development of a sustained yield plan or a plan that alters the different areas at different times. Third, single species management might be instituted for important species, endangered species or others. Finally, selective techniques discussed in this paper might be used to maintain nongame bird communities in habitats managed for other purposes, such as timber harvest.

The manager must consider the size of the habitat that is being managed and the natural successional sequence. In addition, unusual species must be considered. It is difficult to attract rare or unusual species to a forest habitat by selective management. Knowledge of the habitat requirement of the avian community and major species make for the most effective management of the north central forests for nongame birds.

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APPENDIX 1

Common Name	Scientific Name
Killdeer	*Charadrius vociferus*
Barred Owl	*Strix varia*
Downy Woodpecker	*Picoides pubescens*
Black-backed Three-toed Woodpecker	*Picoides arcticus*
Great Crested Flycatcher	*Myiarchus crinitus*
Alder Flycatcher	*Empidonax alnorum*
White-breasted Nuthatch	*Sitta carolinensis*
Red-breasted Nuthatch	*Sitta canadensis*
Brown Creeper	*Certhia familiaris*
Gray Catbird	*Dumetella carolinensis*
American Robin	*Turdus migratorius*
Starling	*Sturnus vulgaris*
White-eyed Vireo	*Vireo griseus*
Yellow-throated Vireo	*Vireo flavifrons*
Warbling Vireo	*Vireo gilvus*
Black-and-white Warbler	*Mniotilta varia*
Nashville Warbler	*Vermivora ruficapilla*
Cape May Warbler	*Dendroica tigrina*
Yellow-rumped Warbler	*Dendroica coronata*
Black-throated Green Warbler	*Dendroica virens*
Kirtland's Warbler	*Dendroica kirtlandii*
Ovenbird	*Seiurus aurocapillus*
Canada Warbler	*Wilsonia canadensis*
American Redstart	*Setophaga ruticilla*
House Sparrow	*Passer domesticus*
Brewer's Blackbird	*Euphagus cyanocephalus*
Cardinal	*Cardinalis cardinalis*
Savannah Sparrow	*Passerculus sandwichensis*
Slate-colored Junco	*Junco hyemalis*
Chipping Sparrow	*Spizella passerina*
Lincoln's Sparrow	*Melospiza lincolnii*
Swamp Sparrow	*Melospiza georgiana*

NORTHEASTERN AND NORTH CENTRAL FOREST TYPES AND THEIR MANAGEMENT

Lewis F. Ohmann[1]

ABSTRACT.--A brief background is given of the forests of the north-central and northeastern United States. Then, the major forest types, typical timber management objectives, and common silvicultural practices used in these forests are described.

Management of forests of the north-central and northeastern United States for wood products affects a wide variety of habitats for nongame birds. Therefore, a familiarity with the major forest types and how they are managed is desirable to fully understand these forests as habitats for nongame birds. This report briefly outlines the major forest types, the principal forest products, and the typical silvicultural practices of this region.

BAILEY'S ECOREGION CLASSIFICATION

Because many of the forest types occur over the entire area--for example, northern hardwoods are found from Minnesota to the east coast--I will use Bailey's (1978) hierarchial classification system (ECOREGION) to characterize the region in broader, more generalized terms before describing the types. In Bailey's system, the north-central and northeastern United States are classified within the Humid Temperate Domain (fig. 1); a mid-latitude zone where the presence of both tropical and polar air masses cause large seasonal changes in temperature and precipitation. Forests are a mixture of evergreen needleleaf and deciduous broadleaf trees (Bailey 1978). The Domain is subdivided into two areas--the Warm Continental and the Hot Continental.

In the eastern United States, the Warm Continental Division is synonomous with the Laurentian Mixed Forest Province. This Province occurs between latitudes 40° and 55° North and extends from the continental interior to the east coast. It is made up of the north-central Lake-Swamp-Moranic Plains and the Adirondack-New England Highland landforms. The entire area was glaciated during the Pleistocene and thus lakes, poorly drained depressions, moranic hills, drumlins, eskers, and outwash plains are common. Elevations within the province are generally from sea level to 4,000 feet with a few peaks of above 5,000 feet. Rolling hills of low relief characterizes most of the area, but the mountains of the Adirondack-New England Highlands have reliefs of 1,000 to 3,000 feet. Winters are cold and moderately long and snow cover is usually present all winter. Summers are warm--more than 120 days of temperature above 50°F.--but the growing season is short and the frost-free period is from 100 to 140 days. Precipitation ranges from 24 to 45 inches with a maximum in the summer and no dry seasons (Bailey 1978).

The vegetation of the Province is transitional between the boreal forests to the north and the deciduous forests to the south and is composed of stands of mixed coniferous-deciduous species, or mostly pure deciduous stands on favorable sites, and mostly pure coniferous stands on less favorable sites (Bailey 1978). The pines and many of the deciduous species are pioneers that follow fire or abandonment of cleared land. Four plant association sections are recognized within the province: Spruce-Fir, Northern Hardwoods-Fir, Northern Hardwoods, and Northern Hardwoods-Spruce (figs. 1 and 2).

The Hot Continental Division lies immediately adjacent to the Warm Continental Division The boundary between the two is the 72°F. warmest-month isotherm. The landforms comprising the Eastern Deciduous Forest Province of this Division are the East-central Drift and Lakebed Flats, the Eastern Interior Uplands and Basins, and the Appalachian Highlands. Only the northern parts of the Province were glaciated. Elevations range from sea level to 2,500 feet with a few peaks above 4,500 feet. Most of the area is rolling and has low relief, but in the Appalachian Highlands relief is as much as 3,000 feet. The climate is one of cool winters and hot summers with 35 to 60 inches of annual precipitation and a maximum in summer. The vegetation is primarily deciduous broadleaf--northern hardwoods or oaks--and conifers at higher elevations. On low, wet areas, the vegetation is primarily bottomland hardwoods and spruce. The plant association sections that make up the Province are the Maple-Basswood and Oak Savanna, Beech-Maple, Mixed Mesophytic, Appalachian Oak, and Oak-Hickory (figs. 1 and 2).

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- DOMAIN (2) HUMID TEMPERATE
  - DIVISION (21) WARM CONTINENTAL
    - PROVINCE (211) LAURENTIAN MIXED FOREST
      - SECTION (2111) Spruce-Fir
        - (2112) Northern Hardwoods-Fir
        - (2113) Northern Hardwoods
        - (2114) Northern Hardwoods-Spruce
  - DIVISION (22) HOT CONTINENTAL
    - PROVINCE (211) EASTERN DECIDUOUS FOREST
      - SECTION (2211) Mixed Mesophytic
        - (2212) Beech-Maple
        - (2213) Maple-Basswood and Oak Savanna
        - (2214) Appalachian Oak
        - (2215) Oak-Hickory

Figure 1.--*Ecoregion classification of northeastern United States forests (Bailey 1978)*

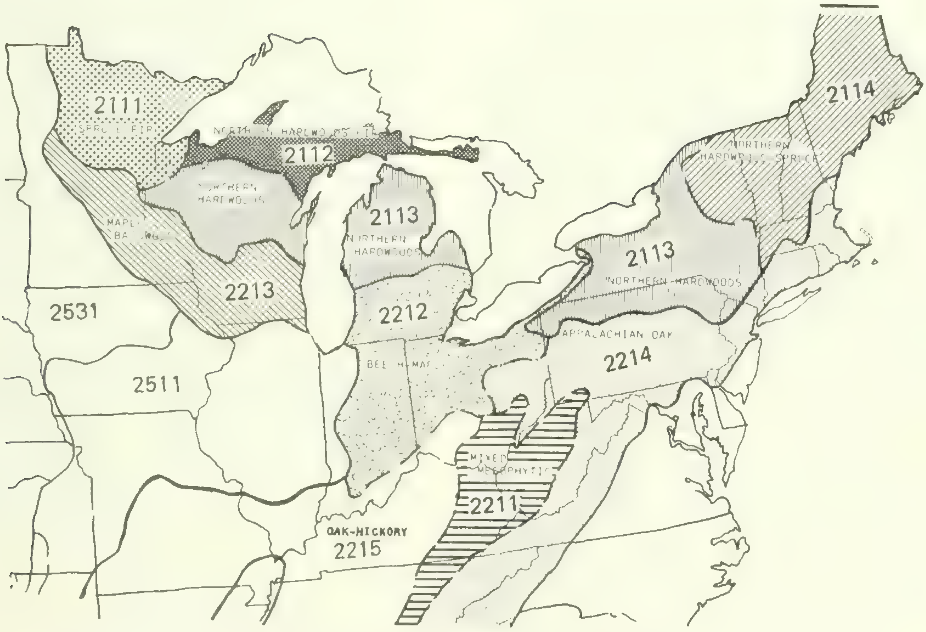

Figure 2.--*Forest types of the north-central and northeastern United States according to Bailey's 1978 Ecoregion classification.*

MANAGEMENT SYSTEMS

Forest land is managed primarily by cover type and the types are based on the majority of trees in the stand. Those typically listed for the north-central region are jack pine, red pine, aspen, northern hardwoods, and black spruce. The principal northeastern types are spruce-fir, eastern white pine, northern hardwoods, cherry-maple, and Appalachian mixed hardwoods. Other types that are important in one or both regions are northern white-cedar, cove hardwoods, oak-pine, and lowland (bottomland) hardwoods.

Many of the forest types in the north-central and northeast are dominated by shade-intolerant species characteristic of early succession, and thus lend themselves best to even-aged silvicultural systems. Under even-aged management the goal is to regenerate and culture stands that are about the same age (all desired trees receive the same amount of direct sunlight during regeneration and growth of the stand). Even-aged management can be a clearcut at rotation age followed by regeneration of the stand through direct seeding, as is common for jack pine; through planting, as is common for red pine; or through allowing resprouting, as is common for aspen. Even-aged management can also include leaving shelterwood or seed trees when harvesting near the end of a rotation to provide natural regeneration, followed by removal of the shelterwood trees or seed trees after the new stand is established.

Even-aged silvicultural practices range from a "let-grow" policy to intensive managemant where both noncommercial and commercial thinnings are made prior to final harvest (Ohmann *et al.*1978). The intensity of management depends on species composition, stand condition, site quality, markets, and management objectives for resources other than wood products.

Forest types composed of tolerant species (sugar maple, beech, spruce, or fir) are often managed under uneven-aged (all-aged) systems. The usual harvest method under this system is to periodically remove selected mature and immature trees either singly or in small groups. Regeneration occurs almost continuously, thus creating an uneven-aged stand of trees of different ages or sizes intermingled either singly or in small groups. The single tree selection method in mixed species stands leads to an increase in the proportion of the more shade-tolerant species in the stand. The group selection method can be used to maintain a higher proportion of less shade-tolerant species.

FOREST TYPES

Presented below are the principal forest cover types of the north-central and northeastern regions, the Ecoregion and Kuchler (1964) plant associations in which they may occur, the typical timber products desired from them, and the usual silvicultural practices used to meet the timber objectives. More detailed information about each type can be found in the management guides from which the data was summarized.

Jack Pine

The jack pine (Benzie 1977a) type occurs primarily in the north-central region where it occupies about 2.5 million acres. It is found in the Spruce-Fir, Northern Hardwoods-Fir, and the Northern Hardwoods Ecoregion Sections (fig. 2) and in Kuchler's Great Lakes Pine Forest type.

Jack pine grows in both pure and mixed stands. Common associates in mixed stands are red and eastern white pine, aspens, white birch, several oaks (mainly northern red oak and northern pin oak), and spruce-balsam fir mixtures. The type is usually found on level to gently rolling sand plains of glacial outwash, fluvial, or lacustrine origin. It also grows on eskers, sand dunes, rock outcrops, ridges, and glacial lake beds and beaches.

Jack pine is a small, short-lived species that establishes readily on recently burned areas, especially on exposed sand sites. It is less shade-tolerant than any of its principal associates except quaking aspen and white birch. Thus, jack pine is a temporary type that on better sites is replaced by more shade-tolerant species when natural succession is not interrupted by fire. On poor sites, jack pine is more permanent and usually grows in pure stands but may be mixed with northern pin oak. The poorest jack pine sites are largely free of shrubs, the medium sites are characterized by ericaceous low shrubs, and the better sites often have a dense undergrowth of tall shrubs.

Jack pine is one of the few species that is generally not re-established where it grows best. Typical timber management objectives are to maintain the type where it is the best-suited species and to replace it at the end of rotation with more productive species (such as red pine) on sites where it is not the best-suited species. Most stands are managed for pulpwood, but stands on the best sites (SI=60+) may be managed for poles or small sawtimber with intermediate thinning.

The preferred silvicultural practice for the type is even-aged management with a regeneration harvest through clearcutting. This is followed by preparing the site through mechanical scarification, chemical control of vegetation, or prescribed burning. Then, the site is planted or seeded (branches bearing serotinous cones are scattered over the area or seeds are dispersed directly on the mineral soil). Jack pine is occasionally regenerated by the seed-tree system if good quality seed trees are available and prescribed burning can be used to prepare the site. Commercial rotation ages are typically 40 to 50 years for pulpwood and on good sites, 60 to 70 years for poles and small sawtimber.

Red Pine

Red pine (Benzie 1977b) occupies about 1 million acres in the north-central region and less than 0.5 million acres in the northeastern region. Although the area of natural red pine forest is small in both regions, it has been greatly expanded by planting. It is found in the Spruce-Fir, Northern Hardwoods-Fir, Northern Hardwoods, and Northern Hardwoods-Spruce Ecoregion Sections (fig. 2) and in Kuchler's Great Lakes Pine Forest type. Naturally occurring red pine is most common on level to gently rolling topography underlain by fine to loamy sands or on low ridges adjacent to lakes and swamps. It grows best on moist, well-drained soils but can withstand moderate drought. In the north-central region, red pine grows in both pure and mixed stands. Associated species on coarse, dry soils are jack pine, aspen, white birch, and northern pin oak. On fine to loamy sands, associates include eastern white pine, red maple, northern red oak, and white spruce-balsam fir mixtures.

Typically, red pine stands are managed intensively to produce pulpwood, posts, poles, cabin logs, and small sawtimber from intermediate thinnings, and high-quality sawtimber and veneer logs from the final crop.

The preferred silivicultural practice is even-aged management with periodic thinnings and a final regeneration harvest through clearcutting. This is followed by preparing the site through mechanical scarification, chemical control of vegetation, or prescribed burning and planting seedlings. Red pine is usually released from competing vegetation by the end of the third growing season. Commercial rotation ages range from 60 years (on best sites with thinning) to 120 years.

White Pine

Eastern white pine (Little *et al.* 1973), the mainstay of the early logging era, is now of minor importance as a timber species in the north-central region. Throughout most of the Lake States, it is threatened by white pine blister rust. Thus, white pine is infrequently planted and planting will not widely increase until rust-resistant stock becomes readily available. Naturally occurring white pine is found in scattered stands throughout the north-central region but is most frequently found as a component of other types--as a super-canopy, as scattered individuals, or as a dominant or codominant component of red pine stands. In the north-central region it occurs in the Spruce-Fir, Northern Hardwoods-Fir, and Northern Hardwoods Ecoregion Sections (fig. 2) and in Kuchler's Great Lakes Pine Forest type. White pine remains an important forest type in the northeastern region where it covers about 7 million acres. It occurs in the Northern Hardwood-Spruce and Appalachian Oak Ecoregion Sections (fig. 2). In the northeast, white pine is often a pioneer species in abandoned fields and pastures. Optimum development is on moist, deep loams or on sandy loams of lower slopes, but it also is able to compete on upper slopes and ridgetops. Common associates of white pine include 9 conifers and at least 18 hardwood species. Densely stocked pure or nearly pure stands of white pine in the north-central region have a poorly developed tall shrub layer, and a low shrub layer that is more prominant than the sparse herbaceous ground cover.

White pine is not well suited for pulpwood, so sawtimber is the major timber management objective (other than Christmas trees). Small wood products can be derived from thinnings, tops, and limbs.

The preferred silvicultural practice is even-aged management with an intermediate thinning and a regeneration harvest through clearcutting followed by site preparation and planting. If a final heavy thinning is made during a good seed year about 10 years prior to clearcutting, good natural regeneration can be expected and advanced regeneration will be available at the final harvest. Release from competing vegetation will usually be necessary. The white pine type is also often harvested and regenerated through a two-stage shelterwood system. Commercial rotation age is from 80 to 120 years.

Spruce-fir

The spruce-fir (Gibbs 1973) type occupies nearly 3 million acres in the north-central region and occurs in the Spruce-Fir, Northern Hardwoods-Fir Ecoregion Sections (fig. 2) and in Kuchler's Great Lakes Spruce-Fir Forest type. In the Lake States, balsam fir is typically more abundant within the type than is white spruce. Spruce-fir is considered the climax forest type for a major part of the Lake States occupied by aspen, birch, and associated conifer forests (Ohmann and Ream 1971). In the north-central region, old-growth stands have various mixtures of balsam fir, white birch, and white spruce. These stands may also contain some black spruce, aspen, and northern white-cedar, and a few black ash, red maple, and balsam poplar. If succession is less advanced, white, red, and jack pine may also by associated with the type. Sometimes, small (usually less than 10 acres), scattered stands of pure fir will originate after fire, windstorms, or epidemics of spruce budworm.

In the Lake States balsam fir occurs also as an understory strata within stands of aspen, white birch, jack pine, white pine, and occasionally red pine. In the natural course of succession, these areas will become spruce-fir. Much of the spruce-fir type within the north-central region originated in this manner, particularly on areas that were undisturbed for many years. North-central region spruce-fir stands typically have a well-developed tall shrub layer, a poorly developed low shrub layer, and a ground cover of mosses that predominate over herbs.

The northeastern region spruce-fir type occurs in the Northern Hardwoods-Spruce Ecoregion Sections(fig. 2) and in Kuchler's Northeastern Spruce-Fir Forest type. Red spruce, white spruce, and balsam fir are the principal species in this region. The type covers nearly 11 million acres in New England and New York. Depending on site conditions, stands may contain only the spruces and fir or spruce-fir in various combinations with other conifers and hardwoods. These other conifers include northern white-cedar, eastern hemlock, eastern white pine, and tamarack. The hardwoods include red maple, paper birch, aspen, white ash, American beech, sugar maple, and yellow birch. Red spruce, white spruce, and balsam fir will grow on a variety of soils, including those that are poorly drained.

In both the Lake States and New England regions, the typical timber objective is to manage the better sites for balsam fir pulpwood and white or red spruce sawtimber. In the central Appalachians, red spruce on good sites is managed for large sawtimber and on poor sites is either managed for pulpwood or reserved for recreation and aesthetic purposes.

The preferred silvicultural practice is even-aged management with regeneration harvest by clearcutting narrow strips or small patches so adjacent areas can shade advance regeneration or serve as a seed source if advance regeneration is not present at harvest. Commercial rotation age is about 70 years for pulpwood and 120 to 150 years for sawtimber. Uneven-aged management can be used in all-aged stands or to achieve an all-aged structure. In these cases, selection cutting of single trees or small groups of trees is done every 5 to 20 years.

Black Spruce

The black spruce (Johnston 1977a) forest type occupies about 2.1 million acres in the north-central region. Sixty-eight percent of this acreage is in Minnesota, and the remainder is in the northern parts of Michigan and Wisconsin. The black spruce type is a major source of pulpwood in northern Minnesota. Christmas trees are harvested on a limited scale on sites too poor for growing pulpwood. The type also occurs as scattered stands on low areas within the northeastern region. Black spruce occurs in the Spruce-Fir, Northern Hardwoods-Fir, Northern Hardwoods-Spruce Ecoregion Sections (fig. 2) and in Kuchler's Conifer Bog Forest type.

Black spruce grows in both pure and mixed stands; in some mixed stands it predominates and in others it is important but not predominant--mixed swamp conifer, upland white spruce-balsam fir, and jack pine types.

The black spruce type is found on organic soil in both regions and on mineral soil in the Lake States. Extensive areas of organic soil are found on gently sloping glacial lakebeds or smaller filled lakes associated with the Laurentian Shield, pitted outwash plains, and morainic areas. On both lakebed and filled-lake sites, the growth rate of black spruce is related to the surrounding ground water flow system. The best sites occur where the soil water is continuous with the regional ground water system and thus is enriched with nutrients flowing from mineral soil areas. The poorest sites occur where the soil water is "perched" above and therefore separated from this regional system. The fertility of these latter sites depends mainly on precipitation, which is low in nutrients.

The black spruce type is common on mineral soil only on the Laurentian Shield area of northeastern Minnesota and in a few isolated areas of Upper Michigan. In these areas black spruce grows on gravelly and bouldery loam and on shallow soil over bedrock. It is usually mixed with other species--jack pine, aspen, and balsam fir--but occasionally forms a pure type. Growth is best where the slope is gentle and moisture is plentiful, either from a shallow water table or seepage. South of the Shield, black spruce is occasionally found on sandy soil with a high water table.

Black spruce stands on the best organic soil sites typically have a dense understory of tall shrubs and stands on medium to poor sites have only a few low shrubs and many sphagnum and feather mosses. Pure black spruce stands on mineral soils often have a poorly developed shrub and herb component and an extremely well-developed carpet of moss (Ohmann and Ream 1971).

The typical timber objective for the type is to manage for a sustained yield of pulpwood on good sites (SI >25) and for Christmas trees on poor sites.

The preferred silvicultural practice is even-aged management with a regeneration harvest through clearcutting, followed by broadcast burning to prepare the site for seeding. Cut strips up to 4 chains wide can be naturally seeded but large patches must be direct seeded. Burning of slash is recommended for all brushy sites, sites with heavy slash, and sites containing dwarf mistletoe. Release from competing shrubs and hardwoods on good sites is usually necessary. Commercial rotation age is from 60 to 160 years depending on stand basal area and stem density. On poor sites, Christmas trees can be grown under uneven-aged management with group selection cutting about every 10 years.

Northern White-cedar

The white-cedar (Johnston 1977b) type occurs in both the north-central and northeastern regions and is found in the Spruce-Fir, Northern Hardwoods-Fir, Northern Hardwoods, and Northern Hardwoods-Spruce Ecoregion Sections (fig. 2) and in Kuchler's Conifer Bog Forest type. The type is most common in the north-central region. It occupies 1.9 million acres in the Lake States, most of it (62 percent of the acreage) in Michigan. The remainder occurs in the northern parts of Minnesota and Wisconsin.

Northern white-cedar grows in both pure and mixed stands. In some mixed stands it predominates and in others it is important but not predominant, such as in the mixed swamp conifer, black spruce, tamarack, and black ash-American elm-red maple types.

The northern white-cedar type is found primarily on organic soils in the Lake States, but is also occurs on mineral soils, mainly on seepage areas and limestone uplands.

Organic soil origin, degree of decomposition, and drainage in the upper horizons are good guides to site productivity. The best soils are neutral or slightly alkaline and contain moderately-to well-decomposed organic matter derived from woody plants or sedges. owever, the upper 4 inches on these sites may e poorly decomposed sphagnum or other mosses. The best sites have moving soil water and are usually near streams or other drainageways. In contrast, the poorest sites have poorly ecomposed acid soil, derived from plants such s sphagnum moss, throughout the entire root one. These sites have little water movement nd are often far from drainageways.

Typically, the tall shrub layer is well-developed, and the species composition varies depending on whether the stand is on organic or mineral soil. The low shrub layer and the herb layer are usually poorly developed. Mosses predominate over herbs in the latter, especially on organic soil.

The typical timber management objective is a sustained yield of posts, poles, and sawtimber. Sites less than SI=25 should be managed extensively for small posts.

The preferred silvicultural practic is even-aged management with regeneration harvest through clearcutting narrow strips or small patches and relying on natural seeding (large clearcut patches will require direct seeding). A combination of clearcut and shelterwood (alternate or progressive strips) can also be used. Broadcast burning of slash, except where shelterwood trees are present or where residual stems are to be saved, will help ensure regeneration. Commercial rotation age varies with site and management objective: 100 to 140 years on poor sites; 70 to 90 years for posts on good sites; and 110 to 140 years for sawtimber on good sites.

Aspen

Aspen (Perala 1977) covers about 13 million acres and is the largest and most widely distributed of the forest types in the north-central region. The type also occurs in the northeastern region. It can be found within the Spruce-Fir, Northern Hardwoods-Fir, Northern Hardwoods, and Northern Hardwoods-Spruce Ecoregion Sections (fig. 2) and in Kuchler's Great Lakes Pine Forest, Great Lakes Spruce-Fir Forest, Northeastern Spruce-Fir Forest, and the Northern Hardwoods Forest types. The dominant species is quaking aspen, which is a small to medium-sized tree that can grow in essentially pure stands but usually is found with other species. Common associates are bigtooth aspen, white birch, northern red oak, red maple, balsam poplar, jack pine, balsam fir, spruce, and northern white-cedar.

Aspen occupies diverse soils and sites, and its growth rate varies with soil fertility and available moisture. Aspen has persisted in natural stands largely because of fire. Even where it is a minor component of the stand, aspen's ability to produce abundant root suckers often enables it to become the dominant species after logging or fire. If aspen is already dominant, it easily re-establishes itself after logging, especially when cutting is followed by fire or similar treatments to kill back all vegetation.

Because aspen cannot reproduce successfully under its own shade, it is replaced by other species when natural ecological succession is not interrupted by fires, logging, or windstorms. On dry sites, aspen is succeeded by red maple or oaks. On moist, fertile soils, aspen is followed by balsam fir, white or red spruce, white pine, or northern hardwoods. On wet sites aspen is succeeded by balsam fir, black spruce, or northern white-cedar.

Aspen stands typically contain well-developed shrub and herb layers. Plant species diversity is usually greater in this type than in any of its associated conifer forest types.

Timber management objectives vary with site. For most stands the objective is pulpwood. Good sites (SI>80) can be managed to produce veneer bolts and sawtimber. Poor sites (SI<50) can produce fiber through whole-tree utilization and chipping but can be converted to conifers or other hardwoods at the end of the rotation.

The preferred silvicultural practice is even-aged management with a regeneration harvest through clearcutting followed by natural vegetative sprouting. Clearcuts should be larger than 2 acres. Aspen stands with a northern hardwood understory can be regenerated by clearcutting or can be converted to northern hardwoods by using the shelterwood or selection cutting systems. Commercial rotation age is 35 to 45 years for chipping or pulpwood and 50 to 60 years for veneer bolts and sawtimber.

Northern Hardwoods

The northern hardwood (Tubbs 1977, Filip and Leak 1973) forests cover about 10 million acres in the north-central region and about 15 million acres in the northeastern region. The type can be found in the Northern Hardwoods-Fir, Northern Hardwoods, Northern Hardwoods-Spruce, Maple-Basswood, and Beech-Maple Ecoregion Sections (fig. 2) and in Kuchler's Maple-Basswood, Northern Hardwoods, Northern Hardwood-Fir, and Beech-Maple forest types. The type varies in composition and density depending on soil drainage, past cutting practices, and fire. Characteristic species are sugar maple, American beech, yellow birch, and eastern hemlock. In places basswood, paper birch, white ash, red maple, American elm, and eastern white pine are important associates. On well-drained upland loamy soils in the north-central region, sugar maple is the dominant species and beech, yellow birch, or basswood are the codominant species. On poorly drained sites, hemlock and yellow birch are dominant in the type.

In the northeastern region northern hardwood forests are found up to elevations of about 2,000 feet on rolling or mountainous land. The most productive soils are deep and well- to moderately-well drained.

Typical timber objectives are to manage for high-quality veneer and saw logs where species composition, age distribution, and site productivity allow. Other, less suitable stands are usually managed for pulpwood.

If the objective is to promote composition and yield of the more valuable, less tolerant species (primarily birches), the preferred silvicultural practice is even-aged management with a regeneration harvest through some form of clearcutting and site preparation or a shelterwood cut combined with site scarification and removal of undesirable advanced regeneration. Commercial rotation ranges from 50 to 120 years depending on site, management objective, and intensity of management. If the objective is to promote tolerant species (sugar maple, beech, hemlock, and spruce), uneven-aged management is used with regeneration of the type through selection cutting of individual trees or small groups. Adequate advanced regeneration is almost always present. Periodic cutting will increase composition and yield of desirable trees. Cutting cycles should be about 8 to 12 years in the Lake States and 10 to 20 years in the Northeast.

Cherry-maple

The cherry-maple (Marquis 1973) or Allegheny hardwood type covers about 12 million acres and is a pioneer forest type found within the northeastern region on the Allegheny Plateau of Pennsylvania and New York. It occurs in the Mixed Mesophytic and Beech-Maple Ecoregion Sections (fig. 2) and in Kuchler's Mixed Mesophytic Forest type. It owes its origin to the lumbering and fires of the 1890 to 1920 era in the vast hemlock-white pine-northern hardwoods region of the eastern deciduous forest.

The type is composed primarily of black cherry, red maple, and sugar maple, and common associates are white ash, yellow and sweet birch, American beech, and eastern hemlock. Within this type, black cherry is by far the most valuable species for timber production. Although black cherry grows over a wide geographic area in the eastern United States, it is much more abundant in the Allegheny hardwood area than elsewhere. Ash and maple are two other important timber species of this type.

Because the type occurs on fair to excellent sites, the typical timber objective is to manage for saw and veneer logs. The better the site, the more intensive the management that is economically feasible. On some fair sites, small wood products are the most typical objective (Trimble *et al.* 1974).

When the opportunity exists to manage for the more valuable black cherry and white ash, the preferred silvicultural practice is even-aged management with intermediate thinning at about 30 years and a final regeneration harvest through clearcutting. Commercial rotation age is between 60 and 135 years. When the opportunity for cherry and ash are poor and sugar maple is the best alternative, uneven-aged management with selection cutting of individual trees or small groups of trees is recommended because sufficient advanced maple regeneration is almost always present.

Cove Hardwoods

The cove hardwoods (Trimble 1973), also known as the Appalachian mixed hardwoods, is the most productive hardwood type of the northeastern region. It occurs in the Mixed Mesophytic Ecoregion Section (fig. 2) and in Kuchler's Mixed Mesophytic Forest type. The type is found in the coves and on the moist slopes of the central and southern Appalachian Mountains and adjacent portions of the Allegheny and Cumberland Plateaus.

Cove hardwoods are highly productive and usually occupy good to excellent sites. Soils on these sites are normally deep, medium textured, and well drained and annual precipitation is ample and well-distributed throughout the year. On these rich sites, major species are long lived and can grow to very large sizes.

Stands are characterized by a great diversity of dominant and subdominant species. The species and their proportions vary considerably because of differing past treatments or natural disturbances on sites of different quality, aspect, elevation, and latitude. Species composition ranges from almost pure northern red oak to pure yellow-poplar but generally is a mixture that contains 20 or more commercial species. Important components are yellow-poplar, northern red oak, sugar and red maples, white oak, American beech, white ash, American basswood, black cherry, cucumbertree, sweet and yellow birches hickories, yellow buckeye, and black locust. Many other species occur occasionally, including a few conifers--eastern white pine, red spruce, and eastern hemlock. On good sites at high elevations, the type merges with northern hardwood-black cherry mixtures. On dry sites with shallow soils, the type gives way to oak-hickory.

Because the type grows on the best sites and is the most profitable timber type in the northeast, management objectives are high-quality veneer and saw logs, and small wood products from thinnings, tops, and limbs.

The preferred silvicultural practice is even-aged management with intermediate thinnings and a final regeneration harvest through clearcutting to produce the most desirable mix of species in the new stand. Regeneration for the new stand comes from (1) sprouting from cut trees, (2) advanced regeneration of tolerant and intermediately-tolerant species, and (3) germinating seed, which was stored in the forest floor, from the intolerant yellow-poplar and black cherry. Final harvest rotation may be as short as 60 to 70 years with a heavy thinning schedule and control of tolerant understory at harvest. More typical rotations are from 75 to 105 years. Uneven-aged management through selection cutting of small groups of trees is possible but less desirable because it results in an increase of the less valuable maple and beech.

Oak-Pine

The oak-pine (Trimble *et al.* 1974) type occurs in the northeastern region as part of the Appalachian mixed hardwoods forest at elevations below 3,000 feet. It is found within the Appalachian Oak Ecoregion Section (fig. 2) and in Kuchler's Appalachian Oak Forest type. The five widely-distributed upland oaks in this type are white, northern red, black, scarlet, and chestnut. Although less abundant, the hickories are consistent stand components. Other associates are beech, red maple, sassafras, and sweet birch. Oaks are associated with white pine and pitch pine in parts of the region and with the hard pines in the western and southern parts of the central Appalachians. Oak stands commonly have a poorly developed herb layer and a well-developed shrub/vine strata.

On fair oak sites, management is typically for saw logs (sometimes pulpwood), and small wood products from thinnings, tops, and limbs. On poor oak sites (SI=45 to 54) pulpwood is the usual objective but these sites should probably be converted to pine at the end of the rotation. The management objective for pine is to grow it in pure stands for pulpwood.

The preferred silvicultural practice on fair oak sites is even-aged management with intermediate thinning at 30 to 40 years and a final regeneration harvest through clearcutting if advanced oak regeneration is present. Regeneration of the stand through shelterwood cutting is recommended if no oak advanced regeneration is present. Commercial rotation age may be 70+ years. Uneven-aged management is possible through selection harvest of groups of trees. On poor oak sites either even-aged management with regeneration harvest through clearcutting or converting to pine is recommended. Pulpwood rotation on poor sites is 40 to 60 years. The usual practice for pine is even-aged management with a regeneration harvest through clearcutting. Then, the site is prepared, pine is planted, and in several years the trees are released from competing vegetation regrowth. Commercial rotation age for pine is 40 to 50 years.

Lowland Hardwoods

The lowland hardwoods (Trimble *et al.* 1974) type is also known as the bottomland hardwoods, flood plain hardwoods, or swamp hardwoods. It occurs throughout both regions and varies mostly with the type of landscape on which it occurs. It can be found in all Ecoregion Sections and in Kuchler's Elm-Ash or Northern Flood Plain Forest type. It includes American elm, black willow, green ash, red maple, silver maple, boxelder, and several oak species.

On good sites sawtimber is the usual timber objective and on poor or wet sites pulpwood is the usual objective.

The preferred silvicultural practice is usually even-aged management with regeneration of the type through clearcutting followed by early precommercial treatment to remove undesirable competing shrubs and trees. If pockets of hemlock are present, they can be maintained by a shelterwood harvest with ground scarification. Poor or wet sites, if not converted to spruce, can be regenerated by using the shelterwood system. On good sites in the northern parts of the Lake States, uneven-aged management is recommended with selection harvest of individual trees to prevent shrubs and grasses from invading the site.

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Tuesday Afternoon, January 23

NONGAME BIRD HABITAT MANAGEMENT

Moderator: Roger Holmes
Minnesota Department of
Natural Resources

THE EFFECTS OF CHANGES IN HABITAT ON NORTHERN HARDWOOD FOREST BIRD COMMUNITIES

Barry R. Noon[1], Verner P. Bingman[2], and J. Paige Noon[3]

Abstract.--The effects of habitat change on the avian communities of northern hardwood forests were examined from several perspectives. First, we critically reviewed published reports dealing specifically with the response of birds to habitat change. We then examined bird census data from communities representing varying degrees of habitat disturbance. Specifically, we analyzed census data according to the shape of their rank-abundance distributions and drew inferences about their community structure according to their fit to known distributions.

The consensus of the published accounts that we reviewed is that, over the long term, bird communities are very resilient to habitat change. We generally concur with these findings but with notable exceptions. Most importantly we found that the rare species of undisturbed forests are particularly sensitive to habitat changes. In many disturbed habitats the rare species group is either greatly reduced or completely eliminated. From a conservation perspective, we feel that the normally rare species of undisturbed forests should be of primary concern to forest managers in order to assure their persistence.

INTRODUCTION

It is generally accepted that habitat lection by passerine bird species is most rongly influenced by the structure of the getation (MacArthur and MacArthur, 1961; cArthur et al., 1966; Cody, 1968; Wiens, 69; James, 1971; Shugart and Patten, 1972; derson and Shugart, 1974; Whitmore, 1977; d others). Further, niche separation by ecific habitat selection appears to be the st common mechanism of achieving competi- ve coexistence in temperate bird communi- es (e.g., Shugart and Patten, 1972; James, 71; Whitmore, 1977; Noon and Able, 1978; on, 1979). In light of the apparent inte- al connection between habitat structure d species composition, it becomes very portant to assess the impact of habitat sturbance on avian communities.

From the studies references above one ld predict that habitat alterations, such gging, would result in dramatic changes in bird species composition. However a search of the literature quickly reveals little quantitative information documenting the effects of habitat change on the populations of passerine birds. Hagar's (1960) studies of Douglas-fir forests revealed that logging altered the composition of the bird community and caused a short term decline in the density of breeding birds. Density rapidly returned to pre-cut levels, but the species composition remained changed for many years.

Kilgore (1971) studied the effect on bird species of a large scale reduction in the understory of a giant sequoia forest. He reported only slight changes in species composition, with ground-foraging and ground-nesting birds decreasing and flycatchers and robins increasing. Bird density increased on the disturbed site, however, total breeding bird biomass remained constant.

Hooper (1967, unpublished master's thesis; cited in Webb, et al., 1977) studied clearcut stands in Virginia 6 years after logging. He reported both an increase in species richness and density which he attributed to increased understory development. Conner et al. (1975) studied the effect of clearcutting on the populations of 4 woodpecker species in Virginia. In the absence of snags

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they found this level of logging benefited only one of the 4 species, with the other 3 restricted to less disturbed forests.

Recently, the results of a long-term investigation into the effects of logging on songbird populations in a northern hardwood forest have been reported (Webb et al., 1977). Due to the direct relevance of their research to this symposium, we will discuss the results of their monograph in some detail. In addition, we examine many breeding bird censuses collected from both mature and disturbed hardwood forest communities in order to gain further insights into the apparent correlation between habitat structure and species composition. We conclude by attempting to identify those species groups most negatively affected by habitat disturbance and thus in most immediate need of effective habitat management.

DESCRIPTION OF FOREST TYPE

Northern hardwood forest communities have an ecotonal character, lying south of the pure coniferous forest of the Canadian zone and north of the pure deciduous forest of more austral regions. However, they are not just transitional subclimax forests, but rather represent an extensive climax forest type. Their character alternates between pure deciduous, mixed, and coniferous regions. In the primary deciduous communities the dominant tree species are sugar maple, beech, basswood, yellow birch and red maple. In secondary deciduous communities, aspen, balsam poplar, paper birch, and gray birch are abundant species (Braun, 1950). In northern Michigan and Minnesota the aspen-birch association is the dominant secondary forest type.

The region contains four groups of species (Braun 1950; (after Nichols 1935)): 1) those with distinct southern affinities - beech, white ash, black cherry; 2) those whose northern limit occurs in the northern hardwood zone - sugar maple, basswood and northern red oak; 3) those species which reach their maximal abundance within the northern hardwood forest region - hemlock, white pine, yellow birch and red spruce; and 4) those whose centers of north-south distribution lie within the Canadian zone - white and black spruce, fir, larch, balsam poplar, and paper birch.

The primary mixed communities in north central and northeastern regions are mixtures of northern hardwoods and hemlock. In montane regions of the northeast the primary hardwoods, sugar maple, beech and yellow birch, are mixed with red spruce and in virgin areas with large white pines. In the northeastern zone of the hardwood forest belt the term hemlock-hardwood forest is most applicable. However, in western regions of this zone hemlock is absent and white pine becomes a regular climax dominant (Braun, 1950). In the extreme northern limits of this zone white spruce and balsam fir also achieve dominant status.

Along steep moisture gradients the composition of northern hardwood communities often change rapidly (Fig. 1) giving many areas a mosaic appearance. This pattern greatly increases local bird species diversity. The discrete forest types integrate abruptly into one another and are frequently large enough to maintain regular populations of habitat specialist bird species. This large scale patchiness, particularly pronounced in northeastern hardwood forests, contributes extensively to the high species richness characteristic of these latitudes.

The northern hardwood forest region extends from northern Minnesota and southeastern Manitoba eastward through the upper Great Lake regions, across New England and north to southern Canada (Braun, 1950). It covers most of the Appalachian Plateau in New York and Pennsylvania and has an extensive finger-like projection down the

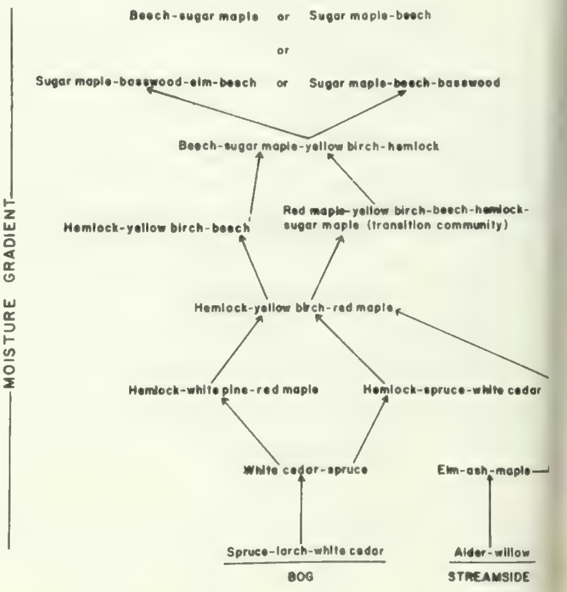

MOISTURE GRADIENT
Beech-sugar maple or Sugar maple-beech
or
Sugar maple-basswood-elm-beech or Sugar maple-beech-basswood
Beech-sugar maple-yellow birch-hemlock
Hemlock-yellow birch-beech
Red maple-yellow birch-beech-hemlock-sugar maple (transition community)
Hemlock-yellow birch-red maple
Hemlock-white pine-red maple
Hemlock-spruce-white cedar
White cedar-spruce
Elm-ash-maple
Spruce-larch-white cedar
BOG
Alder-willow
STREAMSIDE

Figure 1.--Relationship of various forest communities of the northern hardwood region arrayed along a gradient of decreasing water requirements from bog to elevated ridge (after Braun, 1950).

ppalachian Mountain chain into western Mary-and and West Virginia. The cross-hatched egion of Figure 2, labeled coniferous-eciduous forest ecotone, indicates the xtent of this forest type.

THE AVIFAUNA

The reader is referred to Table I for a isting of all the species we encountered in ur survey of 70 breeding bird censuses. he species tabulated are found breeding in ither mature and/or disturbed habitats. Of articular relevance to the topic of our paper re those species which reach their highest requencies in mature forests, those estricted to these habitats, and those most ften encountered as community dominants.

SYNOPSIS OF THE WEBB MONOGRAPH

Webb et al. (1977) studied the long term ffects of different intensities of logging n breeding bird populations. Their study area as within a continuous 15,000 acre northern ardwood forest located in New York's Adirondack ountains. The canopy of this forest was ominated by sugar maple, yellow birch, and eech with hemlock and red spruce comprising a nall, but significant component of the forest.

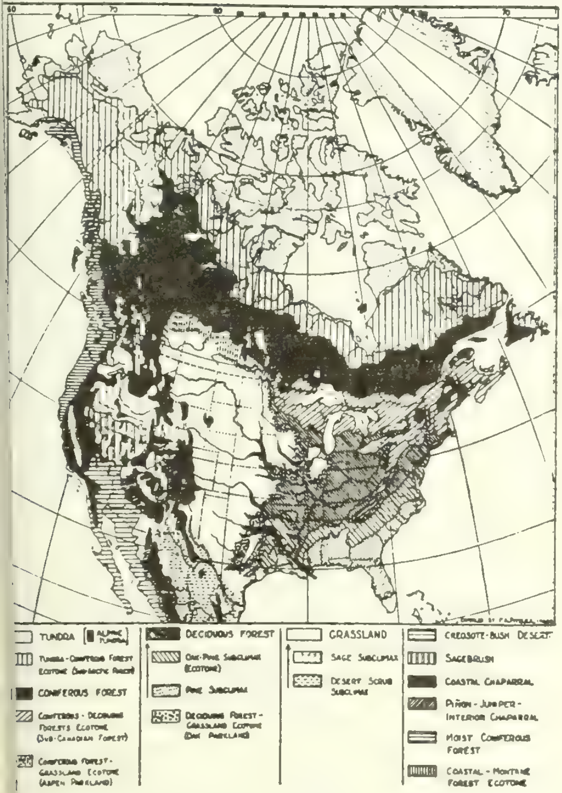

TUNDRA
ALPINE TUNDRA
TUNDRA-CONIFEROUS FOREST ECOTONE (SUBARCTIC FOREST)
CONIFEROUS FOREST
CONIFEROUS-DECIDUOUS FORESTS ECOTONE (SUB-CANADIAN FOREST)
CONIFEROUS FOREST-GRASSLAND ECOTONE (ASPEN PARKLAND)
DECIDUOUS FOREST
OAK-PINE SUBCLIMAX (ECOTONE)
PINE SUBCLIMAX
DECIDUOUS FOREST-GRASSLAND ECOTONE (OAK PARKLAND)
GRASSLAND
SAGE SUBCLIMAX
DESERT SCRUB SUBCLIMAX
CREOSOTE-BUSH DESERT
SAGEBRUSH
COASTAL CHAPARRAL
PIÑON-JUNIPER-INTERIOR CHAPARRAL
MOIST CONIFEROUS FOREST
COASTAL-MONTANE FOREST ECOTONE

Figure 2.--The biomes of North America, vith extensive ecotones and certain sub-regions indicated (after Pitelda, 1941).

Five extensive study sites were selected and subject to 5 levels of treatment. A natural area where no logging was done served as a control. Four areas were logged at 4 different intensities and were identified as the 25, 50, 75, and 100 percent areas. These percentages indicate the approximate amount of commercial timber volume removed when they were first logged. For softwoods the lower dbh limit was 12 inches while for hardwoods the lower limit varied from 14-16 inches dbh. Adirondack forests are particularly well stocked with trees greater than 12 inches dbh (Webb et al., 1977; Noon, unpublished data) and even selective logging results in significant changes in forest structure. The extensive disturbance of at least the 75 and 100 percents areas are still noticeable today (Richard Sage, Jr., personal communication).

Each study site contained 6 censusing stations where every bird seen or heard during a given period of time was tallied. The bird populations on each of the study sites were censused over a 10 year period. Neither the breeding status of individual birds nor the area sampled were determined; thus, only indices of relative abundance of presumed breeders were derived. The sum of the highest number of individuals recorded for a given species at each sampling station became the annual population index for that species for that particular stand. Each species' annual indices were then summer over the 10 annual censuses resulting in a total population index for each species for each stand.

During the 10 year interval a total of 56 species were recorded. However, only those species with a cumulative population index of 50 or above were studied for population trends. This reduced the number of species examined to 26 and excluded, for example, all the woodpeckers, except the yellow-bellied sapsucker, and all birds of prey.

The results of Webb et al. (1977) can be succinctly summarized by noting the effects of logging on:

a) Faunal composition: The fauna on the unlogged area was not supplanted by a different fauna on the logged area. Of the 26 "indicator species" only the veery was never observed on the unlogged control. By contrast, 6 species, ruffed grouse, pileated woodpecker, olive-sided flycatcher, veery, mourning warbler, and chipping sparrow were only recorded on logged sites. Using Spearman rank correlation as an index of shifts in importance value, no significant differences in rank order were observed when each of the treatment stands were compared to the control area. However, a trend of decreasing correlation from lightest to heaviest logging was apparent.

Table 1. Avifauna of the northern hardwood forest region.

	Mature (undisturbed) habitats		Disturbed and successional habitats		
Species (by foraging guild)	Percent of censuses recorded	Percent of censuses dominant	Percent of censuses recorded	Percent of censuses dominant	Changes in species frequency
Foliage gleaners					
Yellow-billed Cuckoo	20		3		
Black-billed Cuckoo	5		20		
Blue Jay	53		43		
House Wren	13		17		
Winter Wren	15		7		
Carolina Wren	15		16		
Catbird	10		32		I[b]
Blue-gray Gnatcatcher	3		13		
Cedar Waxwing	3		27		I
Solitary Vireo	8		13		
White-eyed Vireo	-		7		
Yellow-throated Vireo	43		3		D
Red-eyed Vireo	100	67.5	90	20.0	
Philadelphia Vireo	5		-		
Warbling Vireo	-		13		
Worm-eating Warbler	3		3		
Golden-winged Warbler	-		10		
Nashville Warbler	3		30		I
Yellow Warbler	-		13	6.7	
Magnolia Warbler	5		37		I
Yellow-rumped Warbler	5		10		
Black-throated Green Warbler	55	5.0	40	3.3	
Black-throated Blue Warbler	15		40		I
Cerulean Warbler	48		-		
Chestnut-sided Warbler	10		67	16.7	I
Bay-breasted Warbler	5		-		
Pine Warbler	-		3		
Prairie Warbler	-		10		
Palm Warbler	-		3		
Yellowthroat	8		47	16.7	I
Yellow-breasted Chat	3		17		
Mourning Warbler	8		40		I
Hooded Warbler	40		13		D
Canada Warbler	3		27		I
Red-winged Blackbird	-		20		I
Common Grackle	15		17		
Northern Oriole	3		23		I
Scarlet Tanager	78		43		D
Cardinal	70		20		D
Rose-breasted Grosbeak	45		57		
Indigo Bunting	15		47	10.0	I
Purple Finch	3		10		
American Goldfinch	8		13		
Chipping Sparrow	-		23		I
Field Sparrow	20		17		
Swamp Sparrow	-		3		
Song Sparrow	20		43	6.7	I
Average importance of guild (mean and (standard deviation))	.426 (.088)		.528***[a] (.083)		

Table 1. Avifauna of the northern hardwood forest region. (continued)

	Mature (undisturbed) habitats		Disturbed and successional habitats		
Species (by foraging guild)	Percent of censuses recorded	Percent of censuses dominant	Percent of censuses recorded	Percent of censuses dominant	Changes in species frequency
Ground foragers					
Ruffed Grouse	28		27		
American Woodcock	-		7		
Mourning Dove	15		3		
Yellow-shafted Flicker	45		43		
Common Crow	30		7		D
Brown Thrasher	3		13		
Robin	58		50		
Wood Thrush	80		47		D
Hermit Thrush	13		23		
Swainson's Thrush	15		20		
Veery	18		77	10.0	I
Starling	18		10		
Ovenbird	88	7.5	77	10.0	
Northern Waterthrush	-		3		
Louisiana Waterthrush	35		3		D
Kentucky Warbler	10		10		
Brown-headed Cowbird	65		17		D
Rufous-sided Towhee	58		70	3.3	
Dark-eyed Junco	10		37		I
White-throated Sparrow	8		23		
Average importance of guild (mean and (standard deviation))	.287 (.052)		.352* (.088)		
Salliers					
Eastern Kingbird	5		17		
Great-crested Flycatcher	83		23		D
Eastern Phoebe	43		3		D
Acadian Flycatcher	63	10.0	3		D
Least Flycatcher	20	7.5	23		
Alder Flycatcher	-		13		
Eastern Wood Pewee	93		47		D
Olive-sided Flycatcher	-		7		
Eastern Bluebird	3		3		
American Redstart	60	2.5	20		D
Average importance of guild (mean and (standard deviation))	.155 (.098)		.056**** (.063)		
Bark gleaners					
Black-capped Chickadee	65		57		
Carolina Chickadee	25		3		D
Tufted Titmouse	75		3		D
White-breasted Nuthatch	90		17		D
Red-breasted Nuthatch	3		13		
Brown Creeper	5		7		
Black-and-white Warbler	15		57		I
Average importance of guild (mean and (standard deviation))	.054 (.039)		.039 (.029)		

Table 1. Avifauna of the northern hardwood forest region.

	Mature (undisturbed) habitats		Disturbed and successional habitats		
Species (by foraging guild)	Percent of censuses recorded	Percent of censuses dominant	Percent of censuses recorded	Percent of censuses dominant	Changes in species frequency
Predators					
Cooper's Hawk	8		-		
Marsh Hawk	3		-		
Red-tailed Hawk	15		-		
Red-shouldered Hawk	-		3		
Broad-winged Hawk	13		7		
Screech Owl	10		-		
Great Horned Owl	10		-		
Barred Owl	20		3		
Average importance of guild (mean and (standard deviation))	.006 (.006)		.002* (.005)		
Bark drillers					
Pileated Woodpecker	30		17		
Red-bellied Woodpecker	53		-		D
Red-headed Woodpecker	23		-		D
Yellow-bellied Sapsucker	13		17		
Hairy Woodpecker	95		43		D
Downy Woodpecker	83		27		D
Average importance of guild (mean and (standard deviation))	.052 (.041)		.012**** (.016)		
Hover gleaners					
Golden-crowned Kinglet	3		-		
Parula Warbler	10		3		
Blackburnian Warbler	15		13		
Average importance of guild (mean and (standard deviation))	.015 (.020)		.004* (.012)		
Hawkers					
Whip-poor-will	-		3		
Chimney Swift	-		10		
Tree Swallow	-		10		
Average importance of guild (mean and (standard deviation))	- -		.004 (.010)		
	N = 40		N = 30		

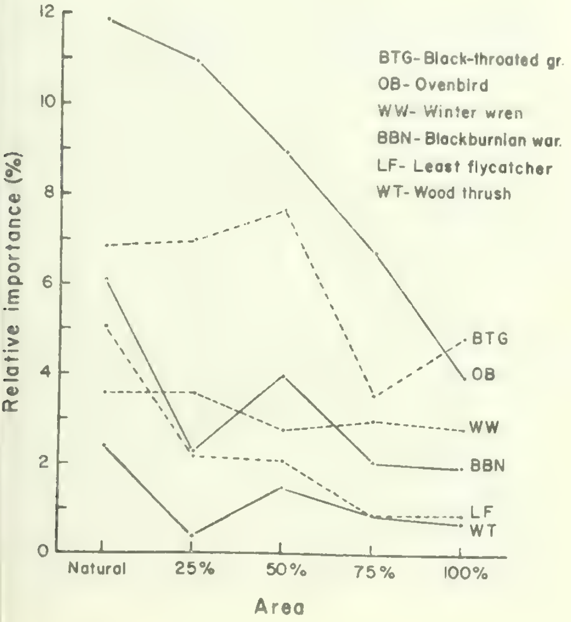
---

[a] *, p<.05; **, .01<p<.05; ***, .005<p<.01; ****, p<.001

[b] I - species frequency increased by at least 20%;
D - species frequency decreased by at least 20%.

b) Diversity: Species richness was lowest on the natural area and increased with logging intensity. However, only at the 2 highest logging intensities was the difference significant. Comparison of the logged stands to the control by their Shannon indices revealed a significant difference only for the 2 highest logging intensities. In both instances these stands had higher diversities, primarily a consequence of the difference in species richness and not evenness. Only the most heavily logged area had a significantly higher evenness.

c) Population trends: Five species showed a negative trend in population size with an increase in logging: ovenbird, black-throated-green warbler, blackburnian warbler, winter wren, and least flycatcher (Fig. 3). The wood thrush had a high population density on the control plot and appeared to be rather equally affected by all levels of logging (Fig. 3). In addition, the yellow-bellied sapsucker responded negatively only to the most intense level of logging. Six species showed a positive trend in population in response to logging: American redstart, chestnut-sided warbler, rose-breasted grosbeak, white-throated sparrow, black-and-white warbler and veery (Fig. 4). Many of the species affected by logging showed trends back towards their pre-treatment levels. Most notable were positive trends for the ovenbird, winter wren and wood thrush and negative trends for the chestnut-sided warbler and white-throated sparrow.



gure 3.--Bird species showing decreasing trends in relative importance as a function of increasing habitat disturbance (modified from Webb et al., 1977).

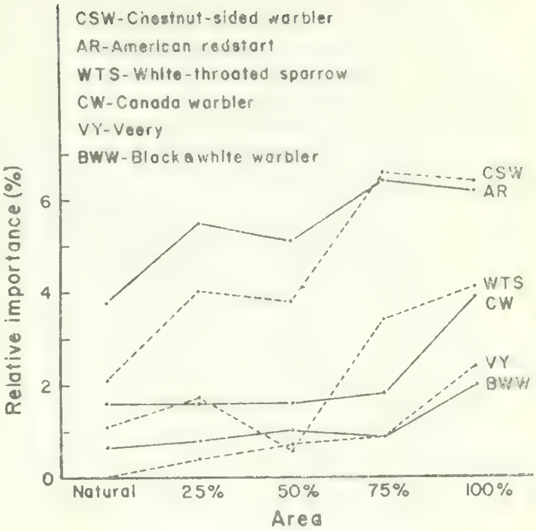


Figure 4.--Bird species showing increasing trends in relative importance as a function of increasing habitat disturbance (modified from Webb et al., 1977).

Webb, et al. (1977) conclude that logging in northern hardwood forests does not completely eliminate any breeding bird species. In addition, their results suggests that over the long term these avian communities are resilient to even severe habitat disturbance. However, we feel that the study of Webb et al. (1977) may suffer from some methodological inadequacies which lead us to question some of their conclusions.

The inadequacies we perceived are outlined below:

a) Population censusing techniques: Their method of calculating a population index not weighted by sampling area undoubtedly over-estimates true abundances. Their method is most problematic in the extensively logged habitats where increased visibility and decreased sound interference would likely result in the observer recording species over a much larger area. As a result, decreases in abundance may go unrecorded.

b) Breeding status unknown: The breeding status of individual birds was not determined and, like the population index, may be most problematic for the disturbed habitats. The logged stands were enclosed within an extensive undisturbed tract of forest which may have resulted in there being more rapid recolonization than would occur in more isolated forest plots. Also, recolonization, especially during the first few years following disturbance, may have been largely by non-territorial individuals excluded from surrounding undisturbed habitats. Stewart and Aldrich (1957) and Hensley and Cope (1951) have supplied evidence that a portion of the population of some species of these forests are composed of a floating population of unmated males. Disturbed, sub-optimal habitats may "collect" these unmated indivuduals.

c) Pooling of data: The only data available to the reader are the pooled population indices. Of most interest are the immediate effects of logging which would only be apparent from individual year censuses. As will become apparent later in our discussion, pooling may mask dramatic year-to-year fluctuations in species composition and relative abundance.

d) Exclusion of rare species: Most of the rare species were excluded from detailed analysis. Threatened or endangered species are most likely part of the rare component of any community. From a conservation perspective these are the species most in need of accurate censusing to determine the effect of various management practices on their populations.

e) Lack of quantitative vegetation data: Only a qualitative description of the forest type was given. As a result it was impossible to unambiguously assess the degree of habitat disturbance. Most lacking was a frequency distribution of trees by dbh size-class before and after logging.

COMMUNITY-LEVEL ANALYSIS

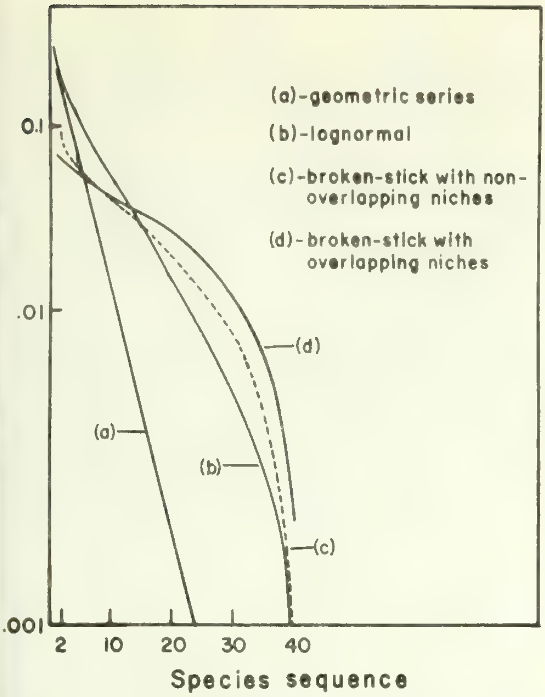
In order to resolve the direct effects of logging on community structure per se, we have analyzed the Webb data (Webb et al., and numerous other censuses in terms of their rank-abundance distributions (MacArthur, 1957, 1960; Whittaker, 1972). In addition to identifying changes in species composition, we analyze the rank-abundance distribution of each of the censuses according to their fit to various theoretical distributions. We then discuss the underlying biological assumptions of these theoretical rank-abundance distributions with regard to specific censuses. Specifically, we are interested in determining the effects on community structure of various intensities of disturbance. In addition, we divided the individual censuses into 1 of 2 groups, mature or disturbed (successional), and examined these data according to changes in the relative importance of various feeding guilds (Table 1).

Over the years avian ecologists have accumulated much information on the relative abundance of species occupying specific habitat types. Many researchers noted that the distribution of relative abundance in communities assumed a few characteristic patterns. Subsequently, models based on the interactions among populations within communities were proposed to account for the observed patterns of relative abundance. Specifically, MacArthur (1957, 1960) proposed several models of relative abundances based on different assumptions about the biological organization of the community.

For 2 of these models a stick, symbolic of a finite resource dimension, was broken into N segments, where N was equal to the number of species. In the first model N-1 points were picked at random along the stick, then the stick was broken at these points. The lengths of the resulting segments were proportional to the relative abundance of the species. In the second model, N independent pairs of points are successively chosen at random locations along the length of the stick. The length of the segment between a given pair of points is proportional to the species abundance. Both broken-stick distributions are specified by a single parameter, the number of species.

The biological assumptions of the first model are that the critical resources are continuously distributed along a single dimension, all resources are utilized, but the species do not overlap in their utilization of the resources (Ricklefs, 1973). The model is restricted to communities comprising a relatively limited number of related species competitively interacting in a structurally homogeneous habitat. This model is often referred to as the non-overlapping niche model (Fig. 5).

The second model assumes a much more even distribution of species abundances. The model rests on the assumption that the abundances of species are independent of each other; that



igure 5.--Theoretical rank-abundance curves fit to 4 major hypotheses: a) geometric series (c = .750); b) lognormal distribution (a = .25, S_0 = 6); c) non-overlapping niche hypothesis; d) overlapping niche hypothesis. All curves were calculated on the basis of 40 species.

s, species do not compete and resources are t fully utilized (Ricklefs, 1973). This del is referred to as the overlapping che model (Fig. 5).

Observed bird species-abundance distritions show their best fit to the nonerlapping niche model (MacArthur, 1957, 60; King, 1964; Longuet-Higgins, 1971). viations from this distribution most equently result from too many common ecies and too few rare species. However, pointed out by Cohen (1966, 1968) and hers, the specific biological assumptions the non-overlapping niche model are not ways supported. Cohen (1968) was able derive this same model by a completely fferent set of hypotheses. Even though e strict biological assumptions of this del are not validated, good fits to this stribution do indicate that some major ctor is being roughly evenly apportioned ong the constituent species of the mmunity (May, 1975).

If the distribution of species relative undance proceeds in a strictly hierarchial shion we arrive at a geometric series stribution. In this model one assumes at the community is dominated by a single factor with a species success determined by its ability to preempt some fraction of the unutilized resources. The most successful species will preempt a fraction k of the resource and the second species a fraction k of the remainder, and so on resulting in a geometric distribution (Fig. 5). This distribution, referred to as the niche preemption model, is usually best fit by data from communities with few species characteristic of an early successional stage or occupying harsh environments (e.g., Whittaker, 1972). The phenomenon of strong dominance usually characterizes such circumstances.

If a variable such as relative abundance is determined by a large number of factors the distribution of that variable will be normal. In communities with many species and large numbers of individuals the distribution of relative abundances is often best described by the log normal (Fig. 5). Communities characterized by this distribution have many moderately abundant species and few common or rare species (Preston, 1948). The biological assumptions underlying this model are obscure and little can be deduced about the structure of communities fit by this distribution. The most consistent condition is the absence of any single, obvious controlling influence on the species' relative abundances.

RANK-ABUNDANCE ANALYSES

Figure 6 presents the rank-abundance results for the data from Webb *et al*. (1977). It is immediately apparent that there is very little difference in the general shape of the distributions. All curves are best fit by MacArthur's non-overlapping niche distribution (hereafter referred to as the broken-stick). The 100% curve also gives a moderately good fit to a lognormal distribution, probably because of this area's extreme heterogeneity represented by 10 years of pooled data. In general, polling of data over many years improved the fit to a broken-stick distribution for all types of forest stands we examined (see below). As mentioned previously, pooled data likely masks any of the immediate effects of logging on community structure.
It would be of great interest to look at rank-abundance distributions for each of the stands on a yearly basis. Unfortunately, the annual data is not available.

These curves deviate from the theoretical broken-stick distributions by having too many common species and too few rare species. However, if broken-stick distributions are calculated on the basis of the number of observed ranks, and not on the number of observed species, all these curves are fit very accurately. Calculations of goodness of fit on

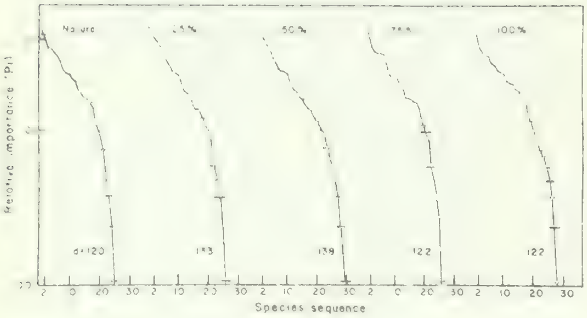


Figure 6.--Rank-abundance curves for the bird communities from the 5 areas of Webb et al., (1977). The d - values indicate the relative importance of the most common bird species, i ($d = n_i/N_{total}$).

this basis seems reasonable: if the populations were perfectly sampled the probability of having 2 species with exactly the same number of individuals would be very small. Perfect sampling increases the number of ranks and usually decreases the dominance resulting in improved fits to the broken-stick distribution.

Rank abundance distributions well fit by a broken-stick model are characteristic of ecologically homogeneous groups of species which randomly apportion amongst themselves a fixed amount of some key resource (May, 1975). The implication from a comparison of these distributions (Fig. 6) is that this apparent mechanism of allocation of a major resource is not disrupted by logging. Our conclusion from this type of community-level analysis corroborates those reached by Webb et al. (1977). Northern hardwood bird communities appear to recover rapidly from habitat disturbance and, despite changes in species composition, community structure remains relatively stable.

Some questions remain, however, about the generality of this conclusion. We have already elucidated what we consider to be methodological difficulties with the Webb data. To unravel the effects of pooled data and to determine whether the conclusions reached by Webb et al. (1977) are consistent with other published data, we examined censuses from several disturbed northern hardwo forest communities. Most of the data were taken from breeding bird censuses published in American Birds (Audubon Field Notes).

When we examined other bird census data to test the generality of Webb's results we found that data directly comparable to their study were scarce. However, bird census data were available from a mature northern hardwoo community both before, and after, logging (Fig. 7) (DeGarmo, 1948, 1953; Chandler, 1958 Harrison et al., 1964; Leitsch, 1968; Smith, 1973). This 15 acre plot, located in West Virginia, was selectively logged of most of its marketable timber in 1955, and we feel closely approximates the 75-100 percent logged areas of Webb et al. (1977) in degree of habitat disturbance.

The shape of the rank-abundance curves both before and after logging are very simila (Fig. 7). Therefore, logging appeared to hav little effect on the overall community organiza tion. All the single year censuses are best fit by geometric series and contrast sharply with the pooled distributions of Webb et al. (1977) (Fig. 6). These communities have low species diversity, high dominance, and

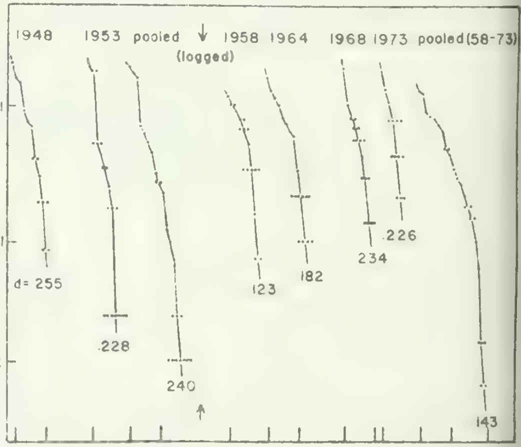


Figure 7.-- Rank-abundance curves for the bird communities of a hardwood forest plot before and after selective logging. Numbers above the curves indicate the year of the census. Pooled curves represent data combined over 2 or more years. d-values as in Fig. 6.

cording to the biological assumptions derlying this model, should be character- ed by a pattern of niche preemption.

Individual year censuses on this plot corded few species and were marked by tensive year to year variability in the lative abundance and presence of the less mmon species. Only by pooling data over ars do the rank-abundance curves approach e broken-stick distribution proposed by cArthur (1957, 1960) as characteristic of mperate bird communities. Turnover of me portion of the rare species each year sults in a much higher apparent species chness when the data are pooled. Up to me asymptotic limit, total species rich- ss of a small plot may be a function of e number of years of study, a consequence a great deal of variability in yearly ecies composition.

Our initial conclusions from these mparisons (Fig. 7) indicate that the avian mmunity structure of this site was little fected by selective logging. However, like the Webb results, there was extensive rnover in species composition. Rufous- ded towhee, mourning dove, and chestnut- ded warbler appeared for the first time the second, fourth, and fifth most minant species, respectively.

In addition, there is a suggestion of greater number of rare species in the disturbed habitat relative to the logged bitat (Fig. 7). This is apparent from e number of ranks falling in the third g cycle. In this regard it may be sig- ficant that the 1948 census comprised ly 7 man-hours and likely underestimated chness, particularly for the rare species.

To further test the sensitivity of re species to logging, and the effects habitat disturbance on northern hardwood rests in general, we contrasted rank- undance curves representing the avian mmunities of mature (undisturbed) forests those from successional and disturbed rests (Figs. 8-10).

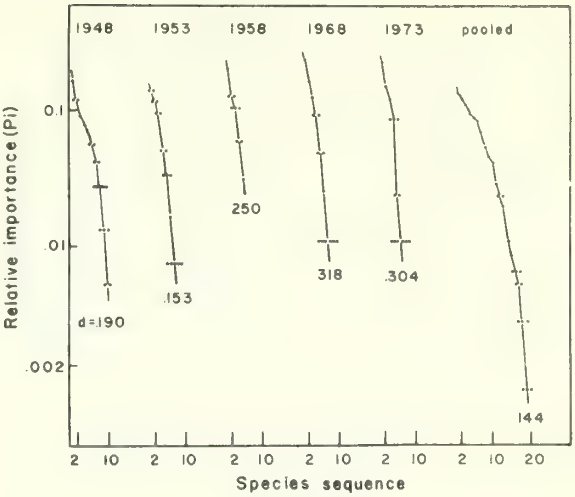


Figure 8.--Rank-abundance for the bird communities of a hardwood forest plot experiencing secondary succession. Labels as in Figs. 6 and 7.

Figure 8 represents a successional quence of an initially disturbed northern rdwood forest in West Virginia. Censusing this 15 acre plot began in 1948 and was ntinued intermittently until 1973 (DeGarmo, 48; Brooks Bird Club, 1953; Baker *et al*., 58; Hutton *et al*., 1968; Eddy *et al*., 73). In 1948 the plot was a thicket with ung trees 15-25 feet tall; by 1968 the ot was a young forest with most trees 8 inches dbh. Especially striking from is figure is that the rank-abundance rves showed no significant change in shape over the 25 year period. As with other censuses, a broken-stick distribution is approximated only by pooling data. In terms of nutrient pools and vegetation structure it may take a northern hardwood forest 60-80 years to recover from severe disturbance (Likens *et al*., 1978). What remains unclear is whether the avian communities of these forests show the same long-term recovery time. Data presented below (Fig. 10) indicates that these bird communities may still be showing the effects of past habitat alteration.

Annual rank-abundance curves are best fit but geometric series, have low species diversities and, in some years, high dominance. All the rank-abundance curves reveal a lack of rare species; i.e., those with relative abundances less than .01. Thus, our suggestion of a sensitivity to disturbance on the part of rare species is further substantiated.

The changes in species composition during succession closely correspond with those reported by Webb *et al*. (1977) for Adirondack forests. Species showing negative trends through succession were the veery, chestnut-sided warbler, mourning warbler, and rufous-sided towhee. Species with consistent positive trends were the wood thrush and black-throated green warbler.

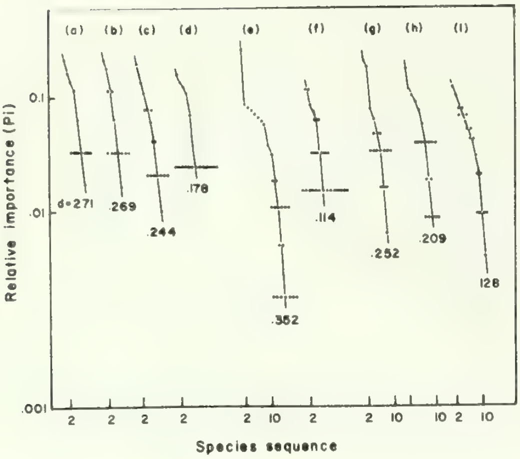


Figure 9.--Rank-abundance curves for the bird communities of successional and disturbed habitats: a-c) deciduous clearcuts 1, 3, and 4 years, respectively, after cutting; d-e) aspen-birch clearcuts 2 and 4 years, respectively, after cutting; f) an early successional hardwood forest; g) mature beech-maple-hemlock forest after an extensive natural disturbance; h) selectively cut-over forest; i) young red maple-gray birch forest. d-values as in Fig. 6.

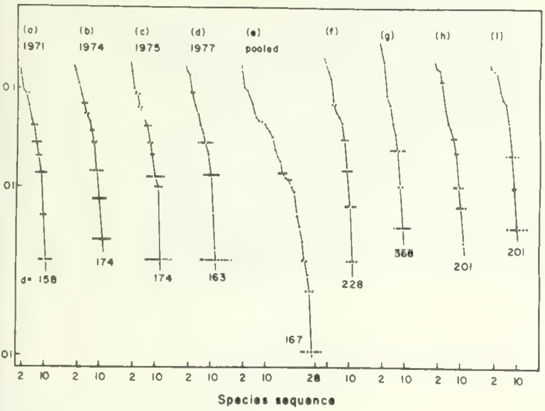
Figure 9 presents rank-abundance curves for early successional and disturbed habitats. With the exception of Fig. 9e, all these single year curves are best fit by geometric series. Dominance varied appreciably, with some disturbed communities having surprising high equitability. The majority of these communities have few rare species, apparent from the figure as a lack of ranks in the third log cycle. A scarcity of rare species seems to be a relatively consistent trend in the disturbed communities that we examined. Figure 9e represents an exceptional case in terms of the extensively disturbed habitats we reviewed. However, it does indicate that a lack of rare species is not a universal response to habitat disturbance.

Admittedly, several of the curves in Fig. 9 illustrate severe habitat disturbance. However, to the extent that these curves convey actual community attributes, they illustrate that the species importance values of the community dominants are relatively immune to changes in habitat structure while the rare species previously occupying these habitats are often eliminat Even though rare species are well represent in Fig. 9e, these species are not those char teristic of mature forests of this region a represent a turnover in the species composition of this group.

Relative to undisturbed forest communities these individual curves indicate little change in community structure (cp. Fig. 10). However, the species composition of many of these communities has changed dramatically. They are dominated almost exclusively by edg species; most notably the chestnut-sided warbler, mourning warbler, rufous-sided towh veery, indigo bunting, and song sparrow. Forest interior birds have been completely eliminated from the heavily disturbed plots. The less severely disturbed forest habitats (Figs. 9g, h, i) remain dominated for the most part by birds characteristic of mature forests, but, significantly, these communiti also show a loss of their rare species.

To substantiate the apparent trend in lo of rare species in early successional or disturbed hardwood forests, we have plotted for comparison a representative sample from bird communities occupying mature, undisturb northern hardwood forests (Fig. 10). These rank-abundance curves contrast most obviousl with the disturbed and successional habitats by the greater number of species whose relative abundances fall in the third log cycle. Thus, rare species appear to contribute substantially more to the species complement of communities of undisturbed forests than they do in disturbed areas. We feel this comparison clearly indicates a sensitivity on the part of the rare species component of undisturbed forests to habitat perturbations (cp. Figs. 7-9).

In agreement with the data from disturbe habitats, these rank-abundance curves are bes fit by geometric series and do not approach broken-stick distributions unless censuses ar pooled over years (Fig. 10e). In addition, even these unperturbed forests show considerable year to year variability in species composition, particularly pronounced as turnover in the identity of rare species. The variance in composition of the rare species group and relative abundances of even the community dominants, appears to be a common feature of the avian communities of north temperate forests.



gure 10.--Rank-abundance curves for the bird communities of mature, undisturbed northern hardwood forests: a-d) a forest plot censused over 4 intermittent years; e) pooled curve for the collective data of curves a-d; f) mature poplar forest; g) mature aspen-northern hardwoods forest; h) northern hardwoods forest; i) aspen-birch forest. Labels as in Figs. 6 and 7.

DISCUSSION

Our examination of the few published udies assessing the effect of forest management on avian communities revealed a lack of gorous documentation of the response of rds to habitat change. From available data g., Webb et al., 1977 and Kilgore, 1971) e implication is that even extensive logng results in few long term changes in rd community composition. This conclusion pears to be in contrast to recent theoreal work establishing a strong relationship tween habitat structure and species compotion. Furthermore, in species rich, equilrium communities the habitat differences rmitting competitive coexistence of similar ecies are often very subtle and perhaps sential to maintain high species richness on 1977; Noon and Able, 1978).

Our comparison of rank-abundance curves, ntrasting mature and disturbed forests in rms of the distribution of species abunnces, largely supports the resilience of mmunity structure. In terms of the fit of ese curves to theoretical distributions we nd little evidence of change in community ructure as a consequence of disturbance. However, large scale changes in species composition occurred after disturbance in many communities. These changes were noted in 2 ways: as a change in community dominants and as a loss of rare species.

In addition, we uncovered some interesting facts pertaining to theoretical concepts of avian community structure. Specifically, we found few annual censuses whose rank-abundance curves conformed to broken-stick (non-overlapping, contiguous niches) distributions. Good fits have commonly been reported for temperate forest bird communities at equilibrium and occupying relatively homogeneous habitats (MacArthur, 1957, 1960; King, 1964). We feel that our selection of censuses meet the criteria of the broken-stick model and the lack of fit represents a real discrepancy.

The data we examined differed most apparently from the broken-stick distributions by having higher dominance, too many common species and too few rare species. As a consequence they were best fit by geometric series. Only by pooling censuses over several years did these curves approach a broken-stock distribution (i.e., Fig. 7). We believe this occurred because of the extensive variability in the composition of the rare species group. By pooling censuses over time additional rare species are accumulated, dominance decreases, and the fit to the broken-stick distribution improves greatly (i.e., Fig. 10e).

The most striking difference we noted in our comparison of mature, undisturbed habitats to disturbed or early successional habitats was a lack of rare species in the latter habitats. This was graphically portraited by there being few, or no, species falling in the third log cycle of rank-abundance curves from disturbed habitats. However, it is important to determine whether this observed difference in rare species is simply a statistical artifact of the data. If mature habitats had significantly higher species richness values or higher breeding densities, or both, these differences could account for the lack of rare species in disturbed habitats. To examine this possibility we have analyzed these (and others) community attributes from both mature and disturbed habitats (Table 2). First note that there is a significant difference in the mean number of species per third log cycle (Table 2). This difference is clearly independent of breeding density, but is complicated by a significant difference in species richness in favor of mature plots (Table 2).

To normalize for the difference in species richness we have independently calculated the percent of species in each census falling in the third log cycle. When we compare these 2 means we find that there is still a signifi-

Table 2. Comparison of avian community attributes of rank-abundance curves (Fig. 7-10) representing mature and disturbed, or early successional, hardwood forest areas. Given are means (standard deviations) and the significance of mean difference where applicable.

Attribute	Mature	Disturbed and Successional
Species diversity	2.567 (.288)	2.464 (.262)
Evenness	0.755 (.028)	0.780 (.064)
Species richness	24.6 (6.6)	17.6 (4.4)**[a]
Density (males per 100 acres)	228.3 (106.6)	198.4 (116.9)
Dominance (n_{max}/N)	0.215 (.062)	0.222 (.068)
No. of species per third log cycle	8.50 (3.75)	1.94 (2.80)***
Percent of species per third log cycle	32.8 (9.0)	9.5 (12.2)****[b]

[a] **, $.005<p<.01$; ***, $.001<p<.005$; ****$p<.001$

[b] arcsin transformation

cant difference in the proportion of rare species (Table 2). Thus, undisturbed plots have both a significantly higher absolute number, and proportion, of rare species.

It is difficult to specifically identify the rare species because of the great variability from site to site in the species composition of this group. However, there do appear to be consistently rare foraging guilds (Table 1). Examining the species composition of these guilds may give us insights into what species are most threatened by habitat disturbance.

The most obvious, and the most readily understood, are the birds of prey. These species are rare even in their preferred habitat, but they seem to be particularly rare in disturbed habitats (Table 1). A second rare foraging guild showing significant decrease as a result of disturbance were the bark drillers (Table 1). Woodpeckers seem to be adversely affected at all but the lightest levels of disturbance. The only woodpecker maintaining a high frequency in logged plots was the ground-foraging flicker. Conner _et al_. (1975) reported similar results from logged habitats in Virginia.

Both the bark gleaner and hover gleaner guilds were consistently rare. Both guilds show decreased frequency in disturbed habitats, but only the hoven gleaner is significant (Table 1). A common factor links many of the species composing the bark gleaner, bark driller, and predator guilds; that is, many of these species are hole nesters. The hole nesters also include a sallier, the great-crested flycatcher, which also showed a large decrease in frequency in disturbed habitats. Hole nesters were also seen to decrease as a result of logging in Finnish forests (Haapenen, 1965). There is a likely correlation between decreases in the woodpeckers, which are primary hole nesters, and secondary hole nesters such as chickadees and titmice which are indirectly dependent upon the presence of primary hole nesters.

Although not a rare guild, the salliers also showed a significant decrease in frequency in disturbed plots (Table 1). The decrease was most pronounced for the great-crested flycatcher, eastern phoebe, acadian flycatcher, eastern wood pewee, and the American redstart. Because most of these species are canopy or sub-canopy salliers their decrease in logged plots is easily understood.

From this admittedly limited (and highly variable) data set we suggest that extensive habitat disturbance may have its most pronounced effects on the rare species of the community. Their consistent rareness even in their preferred habitat is indicative of an extreme specialization to some aspect of their environment. Current evidence from emperate bird species indicates that their ssessment of acceptable habitat is most requently expressed as selection for speci-ic structural features of the vegetation. f rare species normally have more stringent equirements in terms of habitat structure, en their sensitivity to habitat disturbance s easily understood. From a management erspective, identifying the specific require-ents of these birds is of immediate impor-ance and will require essentially an auteco-ogical approach. Until the requirments of ese sensitive species are known, we suggest at the populations of the rare species aracteristic of undisturbed forests be aintained at high levels by preserving tensive tracts of undisturbed forests. rrently, this appears as the sole means assuring their persistence.

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LOWLAND HARDWOOD BIRD COMMUNITIES[1]

Fred B. Samson[2]

Abstract.--Lowland hardwood forests have declined in area since settlement, and precipitous decreases are reported in some states. Suitable silvicultural options for maintaining lowland hardwoods are selection and shelterwood cutting, but clearcutting should be avoided because of soil characteristics. The species-area concept may also be used in acquisition and in management of lowland hardwoods. Resource needs in the breeding or the non-breeding season for birds in the lowland hardwoods are little known nor investigated. Recommendations include preventing further loss of these forests, maintaining a diversity of tree species and stand ages by appropriate silvicultural option, and research to determine bird resource needs particularly during the non-breeding season.

INTRODUCTION

Nearly 50 years ago, Aldo Leopold wrote "The public is (and the sportsman ought to be) just as interested in conserving non-game species, forests, fish and other wildlife as in conserving game." He continued, "In the long run lop-sided programs dealing with game only, songbirds only, forests only, or fish only, will fail because they cost too much, use up too much energy in friction, and lack sufficient volume of support" (Leopold 1930: 287). However, only recently has the awareness and need for integrated management for all wildlife received its due attention. Legislation, including the Environmental Protection Policy Act of 1973, the Endangered Species Act of 1973, Forest and Rangeland Renewable Resource Planning Act of 1976, Land and Waters Resource Act of 1977 and other federal legislative or judicial acts point to the recent increase in professional and public awareness of nongame wildlife. Concurrent with the federal activity has been the passage of legislation or regulations by states supportive of nongame wildlife. Examples include legislation to protect endangered or threatened species (including at least 8 north central or northeast states), "nongame" stamps providing revenues to support research and management of nongame wildlife, and a constitutional amendment passed in Missouri which provides one-eighth of one percent of general sales tax revenues to game and nongame wildlife research and habitat management programs. Finally, as Allen (1973:21) pointed out in the Report to the Committee on National American Wildlife Policy, programs should "recognize that all peoples have a common concern for the survival of plants and animals still existing on earth. We regard this as a feature of the right-to-live concept already advanced. In a utilitarian sense, the preservation of species leaves options open for generations to come, who may find unpredictable uses for many organisms."

Among all terrestrial vertebrates, birds have been particularly successful in exploiting a wide array of aquatic and terrestrial habitats (Dorst 1974). Of these, lowland hardwoods, whether in tropical or temperate latitudes, are particularly important (Ferguson et al. 1975, Pearson 1977, Johnson and Jones 1977, Dickson 1978 and others). The high net productivity of lowland forest trees are influenced by many factors including light, temperature, and the high availability of soil moisture and nutrients (Ricklefs 1973, Whittaker 1975).

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These factors, particularly the availability of nutrients and moisture, have in part contributed to the vast conversion of lowland hardwoods to agricultural crops (Graber and Graber 1976, Korte and Fredrickson 1977, Giulio 1978 and others). Additionally, stream or river channelization for flood control by the Army Corps of Engineers and the Soil Conservation Service and authorized under Public Law 566 has reduced overall acreages of lowland hardwoods. The Soil Conservation Service (1975) has recently reported that over 15,540 km of streams or rivers have been affected, with an additional 18,440 km scheduled for alteration for flood protection. Additionally, applications have been filed for channel modification work involving approximately 91.4 million hectares with planning authorizations issued for approximately 51.8 million of these hectares.

Estimates of presettlement (about 1650) areas of lowland hardwoods are difficult to obtain, but unquestionably these acreages in several northeast and north central states have decreased since settlement (Table 1). Examples of very serious losses include Missouri, wherein about 4% of the presettlement southeastern lowland hardwoods remains today, with only 5860 (0.6%) hectares of the original 971,260 hectares in public ownership (Korte and Fredrickson 1977). In Ohio, less than 5% of an estimated original 80,938 hectares of lowland hardwood remains (Gebhart pers. comm.). Unfortunately, estimates of losses of lowland hardwoods are not available for all states, nor can the overall impact of their loss for wildlife ever be clearly determined. However, studies by Bonnema (1972) in Minnesota, New (1972) in Indiana, and Passordt and Dodge (1975) in Vermont provide examples of the damaging effect of stream modification on wildlife including many nongame avian species.

Currently, there are about 14.3 million hectares of lowland hardwoods in the northeast and north central states (Table 1). Some recent increases in lowland hardwood acreages are evident in New York and Rhode Island, where small farms, no longer economically profitable, are reverting to natural habitats.

FOREST SUCCESSION AND MANAGEMENT

Lowland forests contrast with upland forests in number of tree species present (generally more) and their often patchy distribution (Solomon 1977). These differences reflect the effects of periodic flooding, floods of varying duration, structural damage from ice or debris, and shifts in soil texture and layering as the result of flood activity (Lindsey et al. 1961, Johnson and Bell 1976, Huffman 1977). Of these, Bendinger (1971) described flood frequency and duration as most important in determining distribution of plant species on a flood plain. The irregular horizontal and vertical distribution of the alluvial soils and the dynamic nature of the ecotype influence the relatively high plant species diversity. Tesky and Hinckley (1978), however, have pointed out that these microhabitat characteristics lessen or preclude the opportunity to place lowland hardwoods i the ecoregions or macro-vegetation groupings suggested by the USDA (1949), Kuchler (1964), Braun (1972), and recently by Bailey (1978). The characteristics influence a pattern in lowland hardwood forest succession which is generally similar through most of the northeast and north central states.

Forest succession and composition reflect the interaction of a moisture-nutrient-soil gradient and the shade tolerance of the species forming a plant community (fig. 1). Early successional stages are often characterized by species intolerant of shade yet requiring a moist soil for seed germination. On a flood plain, "new ground" is regularly added through silt deposits. The new soils are often a diverse array of sand of different particle sizes and soil of varying textures. Pioneer tree species, cottonwoods and willows, require a moist mineral soil for seed germination. Because they often are prolific seed producers, they frequently develop into dense stands, competitively eliminating other species. Although tolerant to flooding (Table 2), neither species, particularly the willows, tends to succeed itself due to their shade intolerance. Thus, species more tolerant to shade and flooding including maples (silver and red), boxelder, sycamore, hackberry, ash (green, white, black), and elms form a second stage in succession. Late stages of succession are formed by species intolerant to flooding but shade tolerant including beech, basswood, sugar maple, yellow poplar, white oak in the northeast and north central states and in more southern states hickories, pecans, and several oaks. The time required to evolve to a stable or climax stage for a mesic or lowland stand of shade-tolerant species may exceed that for an upland more xeric stand (Peet and Louks 1977) an important consideration for forest management or modeling. However, soils supporting these late successional stands may be lost to erosion during floods. Thus, the lowland hardwood ecotype is dynamic, with

Table 1.--Estimated area of lowland hardwoods (elm-ash-cottonwood or maple-beech-birch) in north central and northeast states

Locality	Current area (ha)	Percent change during interval	Source
Connecticut	290,290		Dickson and Bowers (1976)
Delaware	32,900		Ferguson and Mayer (1973)
Illinois	335,460	-25 to 28.6, 1962-1973	Graber and Graber (1976)
Indiana	510,600		Spencer (1969)
Iowa[1]	168,500		Ostrom (1974)
Kentucky[1]	926,830		Kingsley and Powell (1978)
Maine[2]	693,650		Ferguson and Kingsley (1972)
Maryland	211,500		Powell and Bowers (1978)
Massachusetts	479,400		Peters and Bowers (1977)
Michigan	769,000	-20.8 presettlement to date	Chase *et al*. (1970); W. B. Bottie (pers. comm.)
Minnesota[3]	515,980	-5 to 10, 1968-1978	W. Hanson (pers. comm.)
Missouri	435,530	-25.5, 1959-1972	Spencer and Essex (1972)
New Hampshire	827,960	-9.5, 1948-1973	Kingsley (1975)
New Jersey	152,570		Ferguson and Mayer (1974)
New York	3,692,000	+10 to 30, 1950-1968	Ferguson and Mayer (1970)
Ohio	4,040	-95, presettlement to date	E. J. Gebhart (pers. Comm.)
Pennsylvania	2,281,260		USDA (1975), J. D. Hassinger (pers. comm.)
Rhode Island	1,200	+25, 1953-1972	D. C. Holt (pers. comm.)
Vermont	1,047,000		Kingsley (1977)
West Virginia	1,389,360		Barnard and Bowers (1977)
Wisconsin	468,600	-56.4 presettlement to 1968	M. E. Reinke (pers. comm.)

[1] Data for only commercial forest lands.

[2] Data for elm-ash-red maple.

[3] Data for two of four management units.

erosion altering late successional stages and with early stages created by the same flood activity.

FOREST MANAGEMENT PRACTICES

Lowland hardwoods can be managed for lumber, water, wildlife, recreation or any combination of these. The management goal(s), species-site relationships, and stand composition determine the approach to regeneration (Dickson 1978).

Selection, shelterwood, and clearcutting are employed (Table 2) in the north central states on well-drained sites where sugar maple-basswood or yellow birch dominate. Selection results in many aged stands and a predominance of shade-tolerant species; whereas, shelterwood with removal of advanced regeneration leads to a moderately tolerant or tolerant species composition (Tubbs 1977). Although clearcutting creates overstory openings, the sand, silt, and clay soils characteristic of floodplains are vulnerable to invasion of grass, herbaceous, or bushy species that may prevent regeneration of desired tree species. On wet sites where red maple, black ash, yellow birch, and elm predominate, individual tree selection is used when timber harvest is the objective (Tubbs 1977).

Suitable silvicultural options in the northeastern states also are influenced by site productivity, species composition, age distribution, and management objectives (USDA 1973). Trees harvested singly or in groups meet recreational or esthetic goals. Even-aged management, primarily clearcutting, results in a mixture of species and is used where light-demanding species are a management objective (Leak and Wilson 1958).

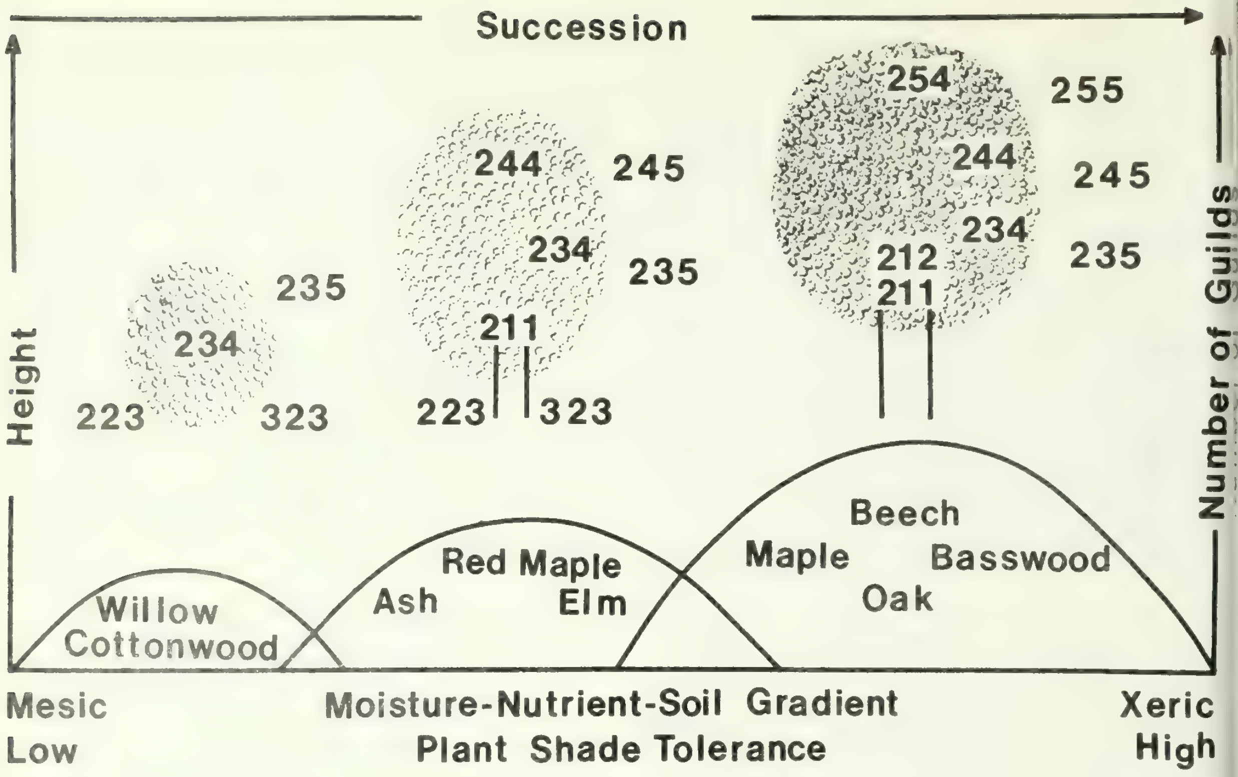

Figure 1.--Relationship of avian guild and forest succession in the lowland hardwoods in the northeast and north central states. Guild membership is listed in Table 3.

Information on shelterwood cutting in the northeast is lacking and its use is therefore limited (Filip and Leak 1973). Management guidelines for lowland hardwoods in the Appalachian oak area have recently been reported in detail by Hooper (1978).

Shade-intolerant species, particularly cottonwoods, but including sycamore and sweet gum, are being managed through clearcutting in Missouri and other southern states. The impact of these monocultures on wildlife is not clearly known, although their value appears less than that of natural diverse stands of lowland hardwoods.

BIRD POPULATIONS IN THE BREEDING SEASON

Species-area Relationships

Plant ecologists for many years have asserted that habitat size is a significant factor in determining numbers of plant species present (Gleason 1922, Cain and Castor 1959, Preston 1960, Greg-Smith 1969, and others). Numerous studies of terrestrial vertebrates on archipelagos or islands (Koopman 1958, MacArthur and Wilson 1967, Diamond 1969, Terborgh 1973, McNeil and Cody 1978, and others) have empirically verified that the number of species can be predicted by area and, in some instances, have discussed the area required for long-term survival of populations. A number of authors also have recently pointed out the usefulness of this concept in the design of wildlife or natural areas (Terborgh 1974, Diamond 1975, May 1975, Slayter 1975, Wilson and Willis 1975, Miller and Harris 1977, and others). Additionally, a number of investigators have provided evidence that size of an inland forest fragment or "island" can be used to predict the number of avian species present (Moore and Hooper 1975, Graber and Graber 1976, Galli _et al_. 1976, Gavareski 1976, Howe and Jones 1977, Tilghman 1977). Although this concept will be covered in detail elsewhere in these proceedings, two land-use implications are important in considering avian use of lowland hardwoods.

Figure 2 depicts a curvilinear relationship between size of a deciduous able 2. Response to flooding or shade and silvical options for major lowland hardwood species. (Response to flooding after: McDermott 1954, Hall and Smith 1955, Wistendahl 1958, Curtis 1959, Lindsey et al. 1961, Dickson et al. 1965, Rochow 1974, Brunk et al. 1975, Solomon 1977, Tesky and Hinckley 1978; silvical options after: USDA Forest Service 1973.)

Species	Response to flooding/shade	Silvical options
oxelder (*Acer negundo*)	Tolerant/intermediate	
ed maple (*A. rubrum*)	Tolerant/intermediate	Selective, shelterwood
ilver maple (*A. saccharinum*	Tolerant/intermediate	Selective, shelterwood
ugar maple (*A. saccharum*)	Intermediate/intermediate	Selective
ellow birch (*Betula alleghaniensis*)	Intermediate/intermediate	Selective, shelterwood
iver birch (*B. nigra*)	Intermediate/intermediate	Clearcut
itternut hickory (*Carya cordiformis*)	Intermediate/intermediate	Group selection
ecan (*C. illinoensis*)	Intermediate/intermediate	Selection cutting
hagbark hickories (*C.* spp.)	Intolerant/tolerant	Group selection
merican beech (*Fagus grandifolia*)	Intolerant/tolerant	Selection cutting
hite oak (*Quercus alba*)	Tolerant/intolerant	Group selection
reen ash (*Fraxinus pennsylvanica*)	Tolerant/intolerant	Selection cutting
lack ash (*F. nigra*)	Tolerant/intolerant	Selective, shelterwood
lack walnut (*Juglans nigra*)	Intolerant/tolerant	Selection cutting
ellow poplar (*Liriodendron tulipifera*)	Intolerant/tolerant	Selection cutting
merican sycamore (*Platanus occidentalis*)	Tolerant/intolerant	Clearcut
astern cottonwood (*Populus deltoides*)	Tolerant/intolerant	Clearcut
wamp cottonwood (*P. heterophylla*)	Tolerant/intolerant	Clearcut
merican elm (*Ulmus americana*)	Tolerant/intermediate	Selective,shelterwood
asswood (*Tilia americana*)	Tolerant/intermediate	Selective
andbar willow (*Salix interior*)	Tolerant/intolerant	
lack willow (*S. nigra*)	Tolerant/intolerant	
wamp white oak (*Quercus bicolor*)	Tolerant/intolerant	Group selection
hite oak (*Q. alba*)	Intolerant/tolerant	Group selection
orthern red oak (*Q. rubra*)	Intolerant/tolerant	Group selection

orest fragment and number of avian species resent in four different forest types. Thus, n order to maintain maximum regional avian iversity (as indicated by each curve in igure 2), top priority should emphasize dentification and protection of large forests ather than an equal area of small forests Forman *et al*. 1976). Second, there is a inimum point (similar to that defined by oodall 1952, Cain and Castor 1959, and reg-Smith 1969) on a species-area curve here a 5% increase in number of avian pecies would require a doubling in size of ne forest fragments. Forman *et al*. (1976) uggested that this minimum point may be seful in size-related land-use decisions nless specific requirements for species that equire even larger forest fragments must be et. Additionally, the configuration of the oodlot may be important; Stauffer (1978) eported a significant relationship between ird species richness and width of stream-side abitat.

Breeding Bird Populations--Precautions

The number of singing males either mapped or incorporated into an index is often the basis for estimating number of territorial males (Williams 1936, Enemar 1959, Robbins 1970) or as the focal point for evaluation of breeding habitat (James 1971, Shugart and James 1973, and others). Yet controversy in use of this technique remains. The interpretation of singing male data relative to the actual number of breeding males or to territorial function is complicated. In some species, song does not have a site-specific territory-related function (Thorpe 1958, Thompson 1960, Baptista 1972, Catchpole 1973, 1977, Marler and Mundinger 1975, Samson 1978, and others). Nor, has the role or function of song in a behavioral-ecological context been examined in detail for many avian species.

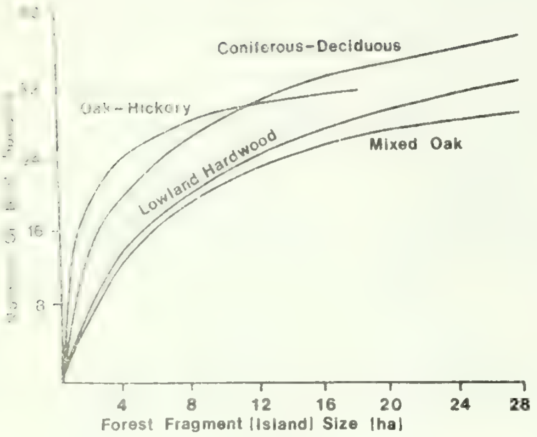

Figure 2.--Avian species--area relationships in four different continental forest habitats at mid-latitudes. Coniferous-deciduous after Moore and Hooper (1975), lowland hardwoods after Graber and Graber (1976), mixed oak after Galli et al. (1976), and oak-hickory after Tilghman (1977).

Additionally, as early as 1961, Thorpe, in an initial important review of avian vocalizations, pointed out that non-breeding males sing more often than breeding males. Studies of a diverse array of species including bobwhite, Colinus virginianus (Stoddard 1931), English robin, Erithacus rubecula (Lack 1946), song sparrow (Nice 1943), snow bunting, Plectrophenax nivalis (Tinbergen 1939), white-throated sparrow (Falls 1969), field sparrow (Best 1977), mourning dove (Baskett et al. 1978), fox sparrow (Martin 1978), prairie warbler, Dendroica discolor (Nolan 1978), and Cassin's finch, Carpodacus cassinii (Samson 1978) support Thorpe's contention. The potential bias of higher singing rates by non-breeding birds on estimates of breeding numbers is not precisely known, but it cannot be disregarded. Recent experimental studies of Orians (1961), Carrick (1963), Jenkins et al. (1963), Nolan (1963), Knapton and Krebs (1974), Power (1975), Samson (1976), and Thompson (1977) as well as "natural experiments" reported by Meunier (1960), Dixon (1963), Delieus (1965), Smith (1978), and others have all reported the existence of non-breeding birds, representing in one study upward to 67% of males present (Best 1975). Thus, considerable caution must be exercised when relating number of singing males to the concept of territory, to number of breeding birds, and to the analysis of breeding habitat.

A final consideration is the effect of events of the non-breeding season on subsequent densities of a breeding population. Lack (1966) argued that annual changes in breeding numbers of birds, both annual residents and migrants, reflected food-related mortality from early fall through winter. Supporting data for parids provided by Lack correlated breeding numbers which changed from year to year to fall mast production, particularly of beech. Subsequent studies by Newton (1964), Fretwell (1969, 1972), Pulliam and Enders (1971), Krebs (1971), Davis (1973), Samson (1976, 1978), Slagsvold (1975), Jones and Ward (1976), and others all support the contention that size of a breeding population reflects or is influenced by the events of the non-breeding season.

Guild-habitat Associations

The analysis of avian communities in different localities has provided insight into concepts of ecological equivalence as well as the association with habitat parameters including the vertical foliage structure (MacArthur and MacArthur 1961), successional stage (Karr 1968, Shugart and James 1973), foliage volume (Willson 1974), horizontal heterogeneity (Roth 1976), and a moisture gradient (Smith 1977). These studies have used a diversity index approach to relate the structure of an avian community to habitat or a multivariate statistical approach to describe avian species or family habitat needs. However, Maguire (1973) and Willson (1974) suggest a detailed analysis of guilds and resource availability may be necessary to clarify the impact of vegetational complexity on avian diversity.

A guild may be defined as "a group of species that exploit the same class of environmental resources in a similar way... without regard to taxonomic position" (Root 1967:335). Advantages of the use of guilds include directing attention toward all species regardless of taxonomic similarity, defining which set of conditions are necessary for a species or group of species to exist in a habitat type, and comparing communities where it is impractical to consider all species using an ecotype. This last advantage of the use of a guild approach is particularly important in reviewing avian use of lowland hardwoods since about 140 avian species may nest in this habitat type. Of the 140 species, raptors and wading birds will be discussed in detail elsewhere in the proceedings.

Breeding bird habitat (fig. 1) in lowland hardwoods can be divided into 3 categories: (1) willow-young cottonwood (early stage of succession), (2) red maple-ash (intermediate stage of succession), and (3) beech-maple-basswood or oak (mature forest, late successional stage). Birds using these habitat categories can be divided by guilds characterized by a 3-digit (ABC) number (table 3) where A is the primary food habit, B is the stratum most often used for foraging, and C is the common foraging behavior.

When willows or cottonwoods or both invade new alluvium, insectivorous foliage gleaning (234) and flycatching guilds (235) accompany insectivore (223) and omnivore ground gleaning (323) guilds (fig. 1). Dependent upon geographic locale, the Kentucky warbler (234), chestnut-sided warbler (234), yellow warbler (234), common yellowthroat (234), white-eyed vireo (234), Wilson warbler (233), Louisiana waterthrush (223), and brown thrasher (323) are among the species of this successional stage. The wood thrush (323), hermit thrush (323), winter wren (234), mourning warbler (234), least flycatcher (235), acadian flycatcher (235), cardinal (334), rufous-sided towhee (334), fox sparrow (334), Lincoln sparrow (334), swamp sparrow (334), song sparrow (334), white-throated sparrow (334) may also nest in brushy areas or in the understory of early to middle successional stages.

When a tree layer develops, several additional guilds are added including an insectivorous (244) and omnivorous (344), while the insectivorous low flycatching (235) may be lost. Examples include the downy woodpecker (211), hairy woodpecker (211), black-billed cuckoo (244), Carolina chickadee (244), black-capped chickadee (244), tufted titmouse (244), and northern oriole (344), depending upon region. As the forest becomes serially mature, additional guilds are insectivorous bark gleaners (212), insectivorous middle canopy gleaners (245), high canopy gleaners (254) and flycatchers (255). The brown creeper (212), white-breasted nuthatch (212), American redstart (245), parula warbler (244), scarlet tanager (254), yellow-throated vireo (254), red-eyed vireo (254), cerulean warbler (254), pileated woodpecker (211), red-bellied woodpecker (211), and great-crested flycatcher (255) are examples depending upon geographic locale. Thus, in lowland hardwoods, there is a stepwise progression evident wherein guilds are added or deleted dependent upon the structure and age of the vegetation. Members of each guild share similar food habits and foraging behavior and stratum, but membership in each guild will vary from location to location as species distribution patterns change.

Nesting Densities

Factors influencing nest site selection are complex in lowland hardwoods. Some species, the common flicker, pileated woodpecker, red-bellied woodpecker, red-headed woodpecker, yellow-bellied sapsucker, hairy woodpecker, and downy woodpecker, excavate a cavity in a dead or live tree or shrub. These cavities subsequently are used by the white-breasted nuthatch, black-capped chickadee, Carolina chickadee, and tufted titmouse. These species may also excavate their own cavities in soft rotting wood. The tree swallow, prothonotary warbler, and great crested flycatcher also will use a natural cavity or an old woodpecker hole (Conner 1978). Along stream banks, the kingfisher excavates a cavity along river bluffs. Other species with specific habitat needs include Swainson's warbler for giant cane (Arundinaria gigantea) and the parula warbler's association with Spanish moss and in northern states with lichen (Usuea sp.) (Eddleman 1978).

The relationship between number of singing males and actual number of nests has been reported for several habitats (Svensson 1974, Jensen 1974) but not in depth in lowland hardwoods. Results of these studies vary from Svensson's (1974) view that mapping of singing males represents a reasonable compromise in estimating breeding population size to Jensen (1974) who, after an in depth study of color-marked individuals of 15 species, concluded that at least in wetlands the mapping method was useless. However, using the mapping method and H', a species diversity index (Shannon 1948), Willson (1974:1018) reported a more diverse avifauna (i.e., a higher BSD) in bottomland forests (1.216-1.158), versus those in grasslands (.478-.727), old fields (.515-.595), upland forests (1.165-1.193) but not in a forest edge (1.272-1.270). Other examples of the diverse lowland difference drawn from the annual singing male census reports (Van Velzen 1975, 1977) include 26 species in 7.6 ha of mature lowland hardwoods in Maryland and 48 species in 18.5 ha of less mature lowland hardwoods also in Maryland versus 24 species per 11 ha and 23 species per 20 ha in upland forests in northern Virginia.

Table 3. Feeding guild and territorial males per 20 ha (raptors and wading birds excluded). Guilds are characterized by a 3-digit (ABC) number where: A = primary food habits (1) seedeater, (2) insectivore, or (3) omnivore; B = stratum most often used for foraging (1) bark, (2) ground, (3) low, (4) middle, or (5) high canopy; and C = common foraging behavior (1) bark drill, (2) bark glean, (3) ground glean, (4) foliage glean, (5) sally, or (6) fruit or buds (after Willson 1974). Number of territorial males are from the thirty-ninth and fortieth breeding bird census (Van Velzen 1975, 1977).

Species	Guild	Number of territorial males per 20 ha habitat, and state
Mourning dove (Zenaida macroura)	123	0.6, mixed mesophytic, OH
Yellow-billed cuckoo (Coccyzus americanus)	244	1.4, beech-oak, OH
Black-billed cuckoo (C. erythrophthalmus)	244	0.2, mixed mesophytic, OH
Common flicker (Colaptes auratus)	323	2.4, ash-basswood, NY
Pileated woodpecker (Dryocopus pileatus)	211	2.4, ash-basswood, NY
Red-bellied woodpecker (Centurus carolinus)	211	7.7, hickory-ash, oak, MO
Red-headed woodpecker (Melanerpes erythrocephalus)	211	4.2, mixed hardwood, MI
Yellow-bellied sapsucker (Sphyrapicus varius)	211	2.8, oak-hickory, OH
Hairy woodpecker (Picoides villosus)	211	1.8, birch-basswood, PA
Downy woodpecker (P. pubescens)	211	1.8, birch-basswood, PA
Great crested flycatcher (Myiarchus crinitus)	255	9.8, red maple-birch, NY
Eastern phoebe (Sayornis phoebe)	235	2.9, birch-maple, CT
Acadian flycatcher (Empidonax virescens)	235	10.9, birch-basswood, PA
Alder flycatcher (E. alnorum)	235	2.3, shrub, NY
Least flycatcher (E. minimus)	235	4.9, ash-basswood, NY
Eastern wood pewee (Contopus virens)	245	27.1, ash basswood, NY
Tree swallow (Iridoprocne bicolor)	234	1.9, maple-pine, ME
Blue jay (Cyanocitta cristata)	334	2.5, ash-maple, NY
Common crow (Corvus brachyrhynchos)	323	2.0, second growth hardwoods, CT
Black-capped chickadee (Parus atricapillus)	244	12.3, ash-basswood, NY
Carolina chickadee (P. carolinensis)	244	7.3, hickory-ash-oak, MD
Tufted titmouse (P. bicolor)	244	5.4, birch-basswood, PA
White-breasted nuthatch (Sitta carolinensis)	212	1.8, birch-basswood, PA
Red-breasted nuthatch (S. canadensis)	212	0.2, mixed mesophytic, PA
Brown creeper (Certhia familiaris)	212	1.8, birch-basswood, PA
House wren (Troglodytes aedon)	234	22.2, ash-basswood, NY
Winter wren (T. troglodytes)	234	0.1, mixed upland, NY
Carolina wren (Thryothorus ludovicianus)	234	3.6, birch-basswood, PA
Gray catbird (Dummetella carolinensis)	234	2.5, ash-basswood, NY
Brown thrasher (Toxostoma rufum)	323	0.7, upland-swamp, MA
American robin (Turdus migratorius)	323	20.0, ash-basswood, NY
Wood thrush (Hylocichla mustelina)	323	20.0, ash-basswood, NY
Hermit thrush (Catharus guttata)	323	3.8, maple-pine, ME
Veery (C. fuscescens)	323	20.0, ash-basswood, NY
Eastern bluebird (Sialia sialis)	335	4.6, red maple, NY
Blue-gray gnatcatcher (Polioptila caerulea)	235	4.8, birch-basswood, PA
Cedar waxwing (Bombycilla cedrorum)	146	2.4, ash-basswood, NY
White-eyed vireo (Vireo griseus)	234	5.0 birch-oak, WV
Yellow-throated vireo (V. flavifrons)	254	6.6, birch-oak, WV
Red-eyed vireo (V. olivaceaus)	254	12.3, ash-basswood, NY
Warbling vireo (V. gilvus)	244	14.8, ash-basswood, NY
Prothonotary warbler (Protonotaria citrea)	234	2.6, flood plain forest, MD
Swainson's warbler (Limnothlypis swainsonii)	234	
Northern parula warbler (Parula americana)	244	1.2, birch-basswood, PA
Yellow warbler (Dendroica petechia)	234	29.6, red maple-birch, NY
Black-throated blue warbler (D. caerulescens)	234	1.3, deciduous-coniferous, VT
Cerulean warbler (D. cerulea)	254	4.8, birch-basswood, PA
Chestnut-sided warbler (D. pensylvanica)	234	4.0, second growth hardwood, CT
Ovenbird (Seiurus aurocapillus)	323	4.9, red maple-birch, NY
Northern waterthrush (S. noveboracensis)	323	3.1, red maple-pine, NY
Louisiana waterthrush (S. motacilla)	223	2.4, birch-basswood, PA
Kentucky warbler (Oporornis formosus)	234	3.6, streamside, PA
Common yellowthroat (Geothlypis trichas)	234	17.3, red maple-birch, NY

Table 3.--Continued

Species	Guild	Number of territorial males per 20 ha habitat, and state
Yellow-breasted chat (*Icteria virens*)	244	26.6, brushy hillside, WV
Mourning warbler (*O. philadelphia*)	234	25.9, ash-basswood, NY
Hooded warbler (*Wilsonia citrina*)	234	0.5, hickory-oak, MD
Wilson's warbler (*W. pusilla*)	233	
American redstart (*Setophaga ruticilla*)	245	19.7, ash-basswood, NY
Common grackle (*Quiscalus quiscula*)	323	17.3, red maple-birch, NY
Brown-headed cowbird (*Molothrus ater*)	323	5.3, hickory-ash-oak, MO
Northern oriole (*Icterus galbula*)	344	22.2, ash-basswood, NY
Scarlet tanager (*Piranga olivacea*)	254	0.6, mixed mesophytic, OH
Cardinal (*Cardinalis cardinalis*)	334	4.9, ash-basswood, NY
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	346	2.5, red maple-birch, NY
Indigo bunting (*Passerina cyanea*)	344	4.9, ash-basswood, NY
Rufous-sided towhee (*Pipilo erythtophthalmus*)	344	12.3, ash-basswood, NY
Chipping sparrow (*Spizella passerina*)	334	7.4, ash-basswood, NY
Field sparrow (*S. pusilla*)	334	1.3, upland forest, NY
White-throated sparrow (*Zonotrichia albicollis*)	334	14.8, red maple-birch, NY
Lincoln sparrow (*Melospiza lincolnii*)	334	
Swamp sparrow (*M. georgiana*)	334	4.1, swamp forest, IN
Song sparrow (*M. melodia*)	334	14.8, red maple-birch, NY

Nesting densities in lowland forests also may exceed other habitats. Examples include 211 singing males per 40.4 ha in a Maryland hickory-oak-ash flood plain forest and 488 per 40.4 ha in a mature deciduous flood plain forest versus 162 per 40.4 ha and 108 per 40.4 ha in an upland oak-hickory forest and upland tulip tree-oak forest respectively in northern Virginia (Van Velzen 1975, 1977). In Pennsylvania, 255 singing males per 40.4 ha were reported in a stream valley-mixed mesophytic forest compared to 163 males per 40.4 ha on a mountain oak-maple forest (Van Velzen 1975, 1977). Carter (1967), Tramer (1969), Blem and Blem (1975), Whitcomb (1977) and Stauffer (1978) also have reported increases in density of breeding birds from herbaceous habitats, to upland, to flood plain habitats.

Nesting Habitat

Although habitat selection by singing males has been examined in several habitats, few published reports describe nest site selection or habitat factors that affect success of open nesters in lowland hardwoods (Stauffer 1978). It also is difficult to characterize habitat in detail for some ubiquitous species (cardinal, American redstart, common crow, and Carolina wren). Additionally, reported habitat use of a species varies from locale to locale. For example, the blue-gray gnatcatcher may prefer a close-canopy forest with little understory (Anderson and Shugart 1974) or may be a habitat generalist (Root 1967, James 1971) rose-breasted grosbeaks may nest in flood plain habitats (Stauffer 1978) or in xeric upland forests (Bond 1957).

For many species, however, the foraging guild encompasses the preferred nesting habitat. The yellow warbler (234), common yellowthroat (234), alder flycatcher (235), Louisiana waterthrush (223), fox sparrow (334), Lincoln sparrow (334), and rufous-sided towhee (334) nest in low shrub willow-bushy areas (Graber *et al*. 1974, Shugart and James 1974). As a tree layer-edge develops, the kingbird (243), black-billed cuckoo (244), parula warbler (244), gray catbird (234), and indigo bunting (344) nest in areas with a variety of life forms including a shrub-stratum, areas of dense saplings, but a poorly-developed canopy. As the forest becomes more xeric or upland in character, nests are found of the bluejay (334), eastern wood pewee (245), brown thrasher (323), yellow-billed cuckoo (244), warbling vireo (244), and northern oriole (344) (Johnston 1947, Johnston and Odum 1956 and others). In tall mature forests, the yellow-throated vireo (254), red-eyed vireo (254), cerulean warbler (254), and yellow-throated warbler (254) nest. Table 3 lists examples of the number of singing males adjusted to individuals per 20 ha for most nesting species found in lowland hardwoods.

BIRD POPULATIONS IN WINTER

Annual residents in lowland hardwoods include the pileated woodpecker, red-bellied woodpecker, yellow-bellied sapsucker, hairy woodpecker, downy woodpecker, white-breasted nuthatch, common flicker, common crow, black-capped chickadee, Carolina chickadee, tufted titmouse, cardinal, and blue jay. Winter woodland residents exclusive of raptors and wading birds, include large flocks of red-winged blackbirds and common grackles which roost in lowland hardwoods, brown creeper, white-throated sparrow, fox sparrow, song sparrow, golden-crowned kinglets, and ruby-crowned kinglets. Some flocks of the pine siskin, purple finch, evening grosbeak, and pine grosbeak also may use lowland forests.

Very little is known of the habitat or energetic requirements of nongame birds in winter. Willson (1970) and Grubb (1975, 1977) have reported the foraging behavior of the white-breasted nuthatch, tufted titmouse, and Carolina chickadee and other species to be influenced by decreased solar radiation, wind velocity, and low temperatures. A pronounced example is the movement of foraging tufted titmice and Carolina chickadees from wooded areas to an old field when temperatures dropped to -20.0 to -29.9 C. The importance of thermal "refuges" such as grape vine thickets or blackberry-hawthorne thickets for these and other species cannot be overemphasized, and additional research on their use is needed. Although some evidence does show that winter movement of song birds, particularly some finches, is influenced by food supply (Bock and Lepthien 1976, Middleton 1977), further research is needed. It is known that artificial feeding (i.e., at winter feeders) can accelerate the onset of breeding (Kallander 1974) to the possible detriment of the species, and the overall effect of food supply and habitat condition in winter-early spring on the density and distribution of breeding songbirds is not clearly known (Knapton and Krebs 1974, Slagsvold 1975).

MANAGEMENT RECOMMENDATIONS AND RESEARCH NEEDS

As in the southeast (Dickson 1978) and west (Johnson and Jones 1977), a major threat to avian species is loss of lowland or stream-riverside habitat through conversion to agriculture, stream channelization, and reservoirs. For example, George (1971) pointed out that 8 of 16 birds that no longer breed in Illinois were residents of the Mississippi River flood plain. The passenger pigeon (Ectopistes migratrius) and Carolina parakeet (Conuropsis carolinensis) are extinct species whose decline in part reflects forest clearing (George 1911, McKinney 1960, Walley 1966). The ivory-billed woodpecker (Compephilus principalis), most certainly extinct in the midwest, and the Bachman's warbler (Vernivora bachmanii), an endangered species, may also have declined as lowland forests and swamps disappeared (Chapman 1932, Tanner 1942). On state endangered species lists, 8 birds in Illinois, 3 in Indiana, 7 in Iowa, 9 in Missouri and New York, 6 in Wisconsin, and 3 in Vermont are associated with lowland hardwoods.

In the management of lowland hardwoods, management or compartment unit size decisions should consider the species-area relationship. As Graber and Graber (1976) point out, this concept may be used in the decision-making process for land acquisition and has been useful in Great Britain (Moore and Hooper 1975) in making recommendations for lands under private ownership. However, this concept assumes a large area will include numerous microhabitats (accounting for more species being represented), but this may not be true. Specific requirements, e.g., cane for Swainson's warbler, mud banks for the kingfisher and bank swallow, bluffs (road-cuts) for the rough-winged swallow, and snags for primary excavators (woodpeckers) and secondary holes (titmouse and others) need to be considered. Conner (1978) has pointed out that many trees selected by primary cavity-nesters are infected by a fungal heart rot or other species of fungi. These trees as well as dead trees or snags should be maintained for both potential nest sites and as a foraging stratum for many species as discussed elsewhere in these proceedings. Additionally, area alone does not predict number of avian species present in some habitats or locales (Johnson 1975, Power 1976, Abbott and Grant 1976) and, although promising in management of lowland hardwoods, future empirical evidence is needed.

Under natural conditions, flood activity and soil erosion will create a natural diversity of the species and age classes. Management of lowland hardwoods characteristic of middle and late successional stage by individual or group selection will result in an interspersion of the species and age classes. Clearcutting should be avoided for these successional stages where limited blocks of clearcuts may be beneficial. In contrast to walnut, basswood, and some other species characteristic of mature forests, the commercial value of willow is negligible. Thus, mechanical treatment, or other approaches may be necessary to regenerate brushy thickets characteristic of early successional stages where natural flooding or erosion are ineffective. However, the conversion of large, uneven-aged stands of hardwoods to plantation plantings of cottonwood, sweetgum or sycamore has at least in the southeast reduced avian use and diversity (Wesley et al. 1976) and therefore should be avoided.

Few published reports describe avian habitat needs in north central and northeast lowland hardwoods in contrast to upland or grassland areas (Wiens 1969, Shugart and James 1973, and others). Studies involving both the breeding and non-breeding season similar to Dickson and Noble (1978) would provide a useful basis to approach other information including habitat characteristics important to nest site selection and nest success. Census techniques employed in these studies should clearly recognize behavioral and ecological problems associated with the interpretation of singing of non-breeding and breeding males. There also is a clear need to establish a mathematical framework for these techniques. For example, of available current techniques, Burnham and Anderson (1976:334, 335) point out "Emlen's approach is not mathematical" (Emlen 1971), but improvements in this and other techniques are becoming available (Kovner and Patil 1974, Burnham and Anderson 1976, and others). Additionally, most studies on the effect of forest management practices have emphasized clearcutting rather than individual or group selection cutting (Adams and Barrett 1976, Whitcomb et al. 1977). Because of the importance of those silvicultural practices in management of lowland hardwoods, their effects on breeding and wintering avian populations should be investigated in depth.

Fretwell (1978:3) has recently commented that "the embarrassing thing about being an avian population ecologist in America today is the distance that separates us from our European counterparts." Fretwell's criticism is directed toward the frequent use of the assumption that birds compete for food during the breeding season to support niche diversification and breeding bird diversity studies. As he emphasizes, this assumption is largely untested, and long term studies to support or refute the assumption are lacking in America. Nor do forthcoming long term studies in Europe provide support. Many European workers, however, have long contended that fall-winter food is the factor limiting population size. Yet, in America, few studies have emphasized resource needs (food or habitat) of forest-dwelling birds overwintering in middle or low latitudes. Considering these important information needs, research on resource needs of nongame birds in the non-breeding season should be emphasized in forthcoming years.

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AVIAN COMMUNITIES AND MANAGEMENT GUIDELINES OF THE ASPEN-BIRCH FOREST

Gary N. Back[1]

Abstract.--Avian communities are discussed in relation to succession of the aspen-birch type. Management guidelines are given, but more information on habitats of stenotopic species is required if comprehensive management plans are to be formulated. Avian management and pulpwood management are generally compatible in the aspen-birch type, but some expenditures may be necessary to maximize bird species diversity.

INTRODUCTION

The aspen-birch type is an extensive and economically important forest type. Its importance to wildlife populations has been recognized for ruffed grouse (Gullion and Svoboda 1972) and white-tailed deer (Byelich, Cook, and Blouch 1972), but little is known about its potential for nongame species. The purpose of this paper is to describe selected bird communities occupying various successional stages of the aspen-birch type and present guidelines for the management of these communities. Emphasis is placed on the aspen-birch type in the north central and northeastern forest regions.

Payne and DeGraaf (1975) described the economic value derived from human enjoyment of nongame birds. They predicted an increase in nonconsumptive recreation associated with nongame wildlife. The need exists to develop nongame management plans and to evaluate effects of the present management practices on nongame species.

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THE ASPEN-BIRCH TYPE

The Society of American Foresters (SAF 1954) define the aspen-birch type as stands in which trembling aspen (Populus tremuloides), bigtooth aspen (P. grandidentata), and paper birch (Betula papyrifera) predominate. They occur in various combinations or in pure stands of any one species. Pin cherry (Prunus pensylvanica) and red maple (Acer rubrum) are common associates. In the eastern U.S. and Canada, 22 tree species are associated with trembling aspen, including balsam popular (Populus balsamifera), balsam fir (Abies balsamea), white spruce (Picea glauca), black spruce (P. mariana), and several northern hardwoods (Folwells 1965).

Beaked hazel (Corylus cornuta) and American hazel (C. americana) are common shrubs in the eastern part of the range of this type. Other shrubs frequently associated with the aspen-birch type are mountain maple (Acer spicatum), speckled alder (Alnus rugosa), green alder (A. crispa), raspberry (Rubus idaeus), gooseberries (Ribes spp.), and willows (Salix spp.) (Folwells 1965, Martin 1959).

Three other types, the aspen, paper birch, and gray birch-red maple types, are descriptively or ecologically similar to the aspen-birch type. The aspen type consists of trembling aspen, bigtooth aspen, and balsam poplar occurring singly, in combination with each other, or in combination with associates pin cherry and paper birch. Balsam fir is common in the understory (SAF 1954).

Paper birch occurs in pure stands or is the predominant species in the paper birch type. Associates include trembling and bigtooth aspen, balsam fir, red spruce (Picea rubens), white spruce, white pine (Pinus strobus), yellow birch (Betula lutea), and others. The understory may be coniferous or include tolerant hardwoods (SAF 1954).

The gray birch-red maple type is not dominated by aspen or paper birch, but is ecologically and structurally similar to the previously described types. A mixture of gray birch (Betula populifolia) and red maple predominate, with gray birch usually more numerous. Trembling aspen, bigtooth aspen, pin cherry, yellow birch, and paper birch are common associates (SAF 1954).

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The four types are combined and referred to as the aspen-birch type in the following discussion except where special reference to a particular type is necessary.

The range of the aspen-birch type is shown in Figure 1. The range was determined by combining the range limits of the four major species: trembling aspen, paper birch, balsam popular, and bigtooth aspen. It includes portions of the boreal, northern hardwood-conifer, and eastern deciduous forests (Aldrich 1963). Because of the extent of the range (approximately 110° of longitude and 30° of latitude) the climatic conditions are quite variable. The type is generally found in areas of long, cold winters with long periods of snow cover and summers that are cool and short (Folwells 1965).

The aspen-birch type is found primarily on uplands of glacial till with a high but moving water table (SAF 1954). Trembling aspen and paper birch develop best on well-drained sandy loams but are found on all but the wettest swamps and driest sands (Folwells 1965). The gray birch-red maple type occupies sand plains as well as heavier-soiled uplands and wet stream margins.

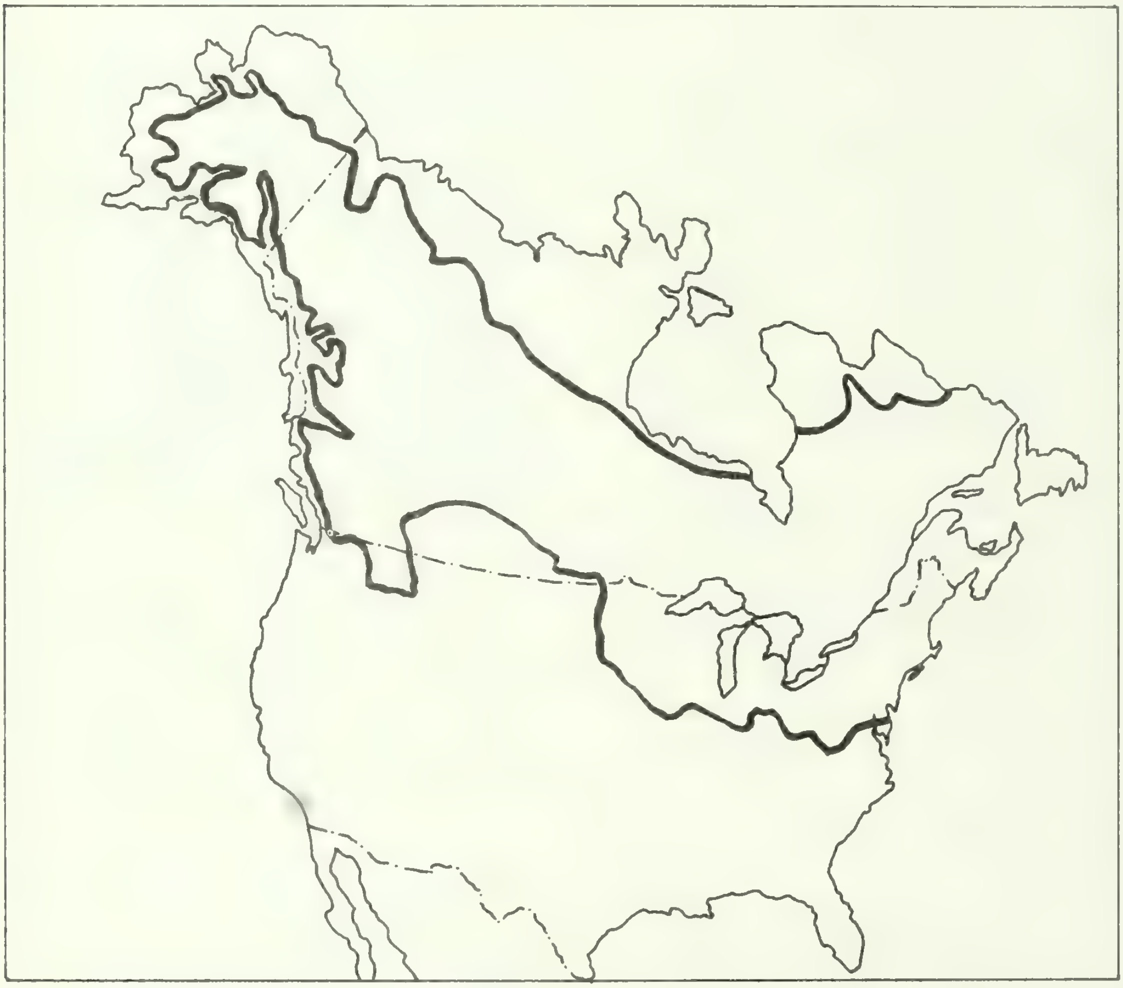

Figure 1.--The range of the aspen-birch type in North America.

SUCCESSIONAL PATTERNS

The aspen-birch type is a relatively short-live pioneer community. Both aspen and paper birch have lightweight seeds[2] which allow long distance dispersal by wind. However, the seeds quickly lose their viability. The seeds of aspen remain viable only two to three weeks under optimum conditions (Moss 1938) and paper birch seeds remain viable for months if the proper moisture conditions are maintained (Joseph 1929). A bare mineral soil is required because the seedling radicle is very delicate and can not penetrate litter (Hutnik 1954). Soil moisture conditions must remain high during the period of germination and root development, as the seedlings quickly succumb to desiccation.

Both species are also capable of vegetative reproduction; root suckering by aspen and stump sprouting by paper birch. The degree of vegetative reproduction depends on a variety of factors of which age and vigor of parent trees, predisturbance stocking, season of disturbance, and degree of canopy destruction are of major importance.

Two natural agents of destruction that were capable of providing suitable conditions for both methods of reproduction in the primeval forests were fire and wind (Cline and Spurr 1942). Heinselman (1973) found that the composition and structure of the presettlement vegetation as well as the vegetation mosaic on the landscape were largely determined by fire for the Boundary Waters Canoe Area in northeastern Minnesota. The aspen-birch type was part of the mosaic. Kittredge (1938) found trembling aspen and paper birch were two of several species with light, windborn seeds or capable of reproduction from underground parts that colonized after fire.

The type which succeeds aspen-birch depends on the nature of the breakdown process, tolerance and stocking level of associate species, and site conditions. Martin (1959) found that in Ontario balsam fir-white spruce succeed aspen-birch after 50-75 years. The spruce and fir are released from the understory as the aspen and birch gradually die out. On xeric sites, northern red oak (Quercus rubra) and bur oak (Q. macrocarpa) replace the aspen-birch (Hansen and Kurmis 1972). On rich, moist sites the beech-birch-maple or maple-basswood type succeed the pioneer type (Stewart and Aldrich 1952, Hansen and Kurmis 1972). In New England, aspen and birch commonly invade abandoned fields along with white pine, which eventually becomes dominant (Cline and Lockhard 1925, Back 1976).

TIMBER MANAGEMENT PRACTICES

The aspen and aspen-birch types account for approximately 35 percent or 17.9 million acres of commercial Lake States forest[3]. Fifty-four percent of the merchantable hardwoods in Canada are aspens (Maini 1972). Aspen and birch together made up 49.2 percent of the total Lake States pulpwood production from roundwood in 1976 (Blyth and Hahn 1978). Paper birch also has value as a veneer quality hardwood in northern New England where it reaches its best development (Folwells 1965).

The silvics of aspen and birch dictate that they should be managed in even-aged stands. Clearcutting to remove merchantable trees followed by elimination of residual stems greater than 1.5 inches (3.8cm) d.b.h. is the basic prescription (Graham, Harrison, and Westell 1963, Marquis, Solomon, and Bjorkbom 1969). The minimum size of the cuts, to be economically attractive, is 10-20 acres (4-8 ha) [3]. The size of the cutting, seedbed preparation, and season of cutting can be altered to favor birch over aspen (Marquis et al. 1969). Intermediate cultural treatments such as cleaning and thinning have been shown to increase growth and yield of aspen (Schlaegel 1972, Hubbard 1972) and paper birch (Marquis et al. 1969). However, economic feasibility requires that the stands have high site index values, potential for veneer or saw quality trees, and are close to the mill (Hubbard 1972).

Prescribed burning following logging has been shown to increase aspen sucker density (Perala 1972) and create favorable seedbed conditions for paper birch and aspen. Although ground fires easily girdle thin-barked paper birch and allow the introduction of wood rotting fungi to fire damaged aspen, the fuel required for crown fires that result in regeneration of the type are not abundant. The shortage of fuel in aspen types prompted Castle and Engle (1972) to suggest that aspen-hardwood types could be used as fuel breaks in pine areas. The conditions required for a high degree of canopy kill in aspen-hardwood types would cause sever fires in other fuel types[4].

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[2] There are approximately 3 million aspen seeds per pound and 1.5 million paper birch seeds per pound (Folwells 1965).

[3] Lundgren, A.L. Economics of aspen management. A paper presented at the joint meeting of Great Lakes Deer Group and the Ruffed Grouse Workshop, Quadna Mt. Lodge, Hill City, MN, Sept. 22, 1970.

BIRD HABITAT ASSOCIATIONS

Breeding Birds

Approximately 116 forest bird species breed in the central and eastern portion of the aspen-birch type. The number of individuals and species vary with several habitat parameters such as habitat patchiness (MacArthur, MacArthur, and Preer 1962, Roth 1976), total foliage volume (Willson 1974), vertical stratification (MacArthur and MacArthur 1961), canopy mixture of hardwoods and conifers (Hooper, Crawford, and Harlow 1973), moisture gradient (Smith 1977), and successional stage (Johnston and Odum 1956, Shugart and James 1973).

For comparative purposes in the following discussion of published literature, the stand development of the aspen-birch type has been divided into three categories: 1) seedling-sapling atage; 2) sapling-pole stage; 3) pole-mature stage.

Seedling-Sapling Stage

The species and density of territorial males reported in six censuses that represent the seedling-sapling stage are given in Table 1. Three species, chestnut-sided warbler (Dendroica pensylvanica), white-throated sparrow (Zonotrichia albicollis), and mourning warbler (Oporornis philadelphia), were present in all six censuses. The same three species and the song sparrow (Melospiza melodia) had the highest densities. The presence of house wrens (Troglodytes aedon) on two of the burned areas may have been due to the availability of cavities in the burned snags (Bergstedt and Niemi 1974). A high density of least flycatchers (Empidonax mimimus) on only one of the burned areas may have been due to a difference in snag density. The 2-year old burn with the high density of least flycatchers had a tree density of 900 per acre (2,220 per ha), of which 90 percent were burned snags (Bergstedt and Niemi 1974). The 3-year old burn had a snag density of 264 per acre (650 per ha) (Niemi 1974a) and a low density of least flycatchers. Yellowthroats (Geothlypis trichas), blackburnian warblers (Dendroica fusca), and rose-breasted grosbeaks (Pheucticus ludovicianus) were found in an island of mature trees within the burned area (Bergstedt and Niemi 1974) and may not be representative of the first development stage.

Of the 36 species recorded in the seedling-sapling stage, 18 species were recorded in only one census. Twenty-four species had maximum densities less than 10 per 100 acres (40 ha). The bird species diversity (BSD) index[5] values were generally low, the highest being 2.50 for the 10-15 year old clearcut.

The dominant tree species of the six census areas was aspen; paper birch was not a major component of any area. The greatest stem density reported was 30,700 aspen suckers per acre (76,000 per ha) on the 3-year old burn (Niemi 1974a). The stands ranged from 3 feet (0.9 m) tall for the 1-year old cut to 10-15 feet (3-4.6 m) for the 10-15 year old clearcut.

Sapling-Pole Stage

Seventeen more bird species were recorded in the sapling-pole stage than in the seedling-sapling stage. Only the ovenbird (Seiurus aurocapillus) and red-eyed vireo (Vireo olivaceus) were recorded in all five censuses (Table 2). Veerys (Hylocichla fuscescens), yellowthroats, and indigo buntings (Passerina cyanea) had higher densities and were recorded in more censuses in the second stage than in the first stage of development. Three species not recorded in the first stage but relatively abundant in the second stage were the black-capped chickadee (Parus atricapillus), catbird (Dumetella carolinensis), and goldfinch (Spinus tristis). The robin (Turdis migratorius) remained about the same density. The white-throated sparrow, chestnut-sided warbler, and song sparrow had decreased densities while the mourning warbler was not recorded in any of the five sapling-pole stage censuses.

The second-growth forest in Vermont, censused two consecutive years by Breault and Farrar (1972) and Farrar (1973), had the greatest BSD value (3.29) and the greatest number of species recorded (36) of the sapling-pole stage. Approximately 50 percent of the tree density was trembling aspen and paper birch and 33 percent was white pine. It was the only census area in which the wood thrush (Hylocichla mustelina) was relatively abundant.

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[4] Sando, R. Burning aspen-hardwood stands. A paper presented at the joint meeting of Great Lakes Deer Group and the Ruffed Grouse Workshop, Quadna Mt. Lodge, Hill City, MN, Sept. 22, 1970.

[5] The bird species diversity index provides a numerical basis for comparing avian communities. It incorporates both the number of species and the abundance of each species present (MacArthur and MacArthur 1961).

Table 1.--Territorial male birds per 100 acres (40 hectares) of six censuses of the seedling-sapling stage.

Species	Stand						Average 7/
	1 yr. old clearcut1/	2 yr. old clearcut2/	2 yr. old burn3/	2 yr. old burn4/	3 yr. old burn5/	10-15 yr stand6/	
Chestnut-sided Warbler	11	24	40	58	42	33	34.7
White-throated Sparrow	32	49	36	20	27	33	32.8
Mourning Warbler	22	54	7	41	27	33	30.7
Song Sparrow	32	32	26			13	25.8
Yellowthroat	11	16		3		20	12.5
Robin	16	5			3	7	7.8
Common Snipe	5	11					
Woodcock	5	5					
Common Flicker		5	3		3		
Red-eyed Vireo			20	10	3		
House Wren			33	17		13	
Brown Thrasher			3		3		
Blue Jay				7	3	7	
Least Flycatcher				37	3		
Hairy Woodpecker				3	3		
Chipping Sparrow				3	6		
Veery				3		7	
Hermit Thrush					3	7	
Swamp Sparrow		5					
Common Grackle			13				
Yellow-bellied Sapsucker				7			
Ruffed Grouse				3			
Blackburnian Warbler				3			
Ovenbird				3			
Rose-breasted Grosbeak				7			
Downy Woodpecker					3		
Black-backed Three-toed Woodpecker					3		
Dark-eyed Junco					3		
Cedar Waxwing					3		
Indigo Bunting					3		
Common Nighthawk					3		
Nashville Warbler						13	
Black and White Warbler						7	
American Redstart						7	
Alder Flycatcher						7	
Red-breasted Nuthatch						7	
Total Density	134	211	181	225	144	214	184.8

1/Minnesota, Niemi 1974b.

2/Minnesota, Niemi 1975.

3/Minnesota, Bergstedt 1973.

4/Minnesota, Bergstedt and Niemi 1974.

5/Minnesota, Niemi 1974a.

6/Minnesota, Doran and Todd 1976.

7/The average was calculated only if a speices occurred in four or more censuses.

Table 2.--Territorial male birds per 100 acres (40 hectares) of five censuses of the sapling-pole stage.

Species	Stand Location					
	Maine1/	N. Dakota2/	Vermont3/	Vermont4/	Saskatchewan5/	Average6/
Ovenbird	20	38	20	8	32	23.6
Red-eyed Vireo	10	55	19	12	13	21.8
Veery	10	65	8	6		22.3
Black-capped Chickadee		10	13	8	2	8.3
Robin	10	5	6	4		6.3
Yellowthroat	45		10	8		21.0
White-throated Sparrow	25		15	16		18.7
Chestnut-sided Warbler	25		19	8		17.3
Catbird	25		17	6		16.0
American Redstart	30		4	6		13.3
American Goldfinch	15	15	2			10.7
Black and White Warbler			12	8	5	8.3
Indigo Bunting	20		2	2		8.0
Downy Woodpecker	15	3		2		6.7
Great Crested Flycatcher		10	4	6		6.7
Eastern Phoebe	15		2	2		6.3
Ruffed Grouse	10		4	2		5.3
Yellow Warbler	40	10				
Song Sparrow	15			2		
House Wren		20	1			
Wood Thrush			22	8		
Blue Jay			12	8		
Rufous-sided Towhee			12	4		
Blackburnian Warbler			8	6		
Brown Thrasher			6	4		
Eastern Wood Peewee			4	2		
Brown Creeper			4	6		
Yellow-rumped Warbler			4	2		
Scarlet Tanager			4	2		
Common Crow			2	2		
Cardinal			2	2		
Rose-breasted Grosbeak			2	8		
Field Sparrow			2	2		
Magnolia Warbler			4		1	
Others	10	114	13	12	38	
Total Density	340	345	259	174	91	241.8

1/Twenty-one year old birch stand, Townsend 1968.

2/Pole stage aspen stand, Clink 1969.

3/Pole stage mixed white pine-paper birch-trembling aspen, Breault and Farrar 1972.

4/Pole stage mixed white pine-paper birch-trembling aspen, Farrar 1973.

5/Young aspen stand, Erskine 1973a.

6/The average was calculated only if a species occurred in three or more censuses.

The aspen forest in Saskatchewan censused by Erskine (1973a) regenerated after a fire. The stand was approximately 30 years old and dominated by trembling aspen. The area had the lowest BSD value (1.64), the least number of species (10), and the lowest density of territorial males (91 per 100 acres) of the five census areas.

Pole-Mature Stage

The ovenbird, red-eyed vireo, and least flycatcher were recorded in all seven censuses of the mature aspen-birch type (Table 3). Mourning warblers which were not recorded in the sapling-pole stage were recorded in the pole-mature stage. The ovenbird, least flycatcher, and Swainson's thrush (Hylocichla ustulata) were more abundant in this stage than either of the first two stages. The red-eyed vireo, veery, black and white warbler, robin, and redstart (Setophaga ruticilla) had about the same abundance as in the sapling-pole stage. Chestnut-sided warblers, white-throated sparrows, black-capped chickadees, yellowthroats, catbirds, and goldfinches all decreased in abundance in the pole-mature stage.

The censuses of the mature stage were scattered from New Brunswick to Saskatchewan. The dominant tree species of four of the censuses were trembling aspen, balsam poplar, and paper birch. Balsam fir and white spruce were the major subdominants (Erskine 1969, 1970, 1971, Price and Speirs 1971).

The greatest BSD value (3.12) and number of species recorded (28) for the mature stage occurred on a Minnesota site dominated by paper birch and red maple (Doran and Todd 1976). Another forest dominated by paper birch in Saskatchewan, however, had the lowest BSD (1.79) and fewest number of species (11) (Erskine 1973b).

The stand censused in Manitoba (Erskine 1972) was the only mature stand in which conifer species were not present. Balsam poplar, trembling aspen, and paper birch were the major canopy species. The understory was also deciduous. The redstart had an estimated territorial male density of 80 per 100 acres, which was more than double the density for any other census of all stages of development.

Successional Trends

The general pattern of bird species diversity through succession is for increased BSD with increased ecological age (Shugart, Anderson, and Strand 1975). The BSD values of the censuses cited above did not follow this general trend. The BSD values tended to increase from the first to the second stage of stand development, but were quite variable in the third stage of development (Table 4). Both the highest and lowest BSD values were obtained from censuses of the sapling-pole stage.

Willson (1974) found the greatest increase of bird species occurred with the initial development of the tree layer and only a small increase as the tree layer developed further. Seventeen more species were recorded on the sapling-pole stage census areas than on the seedling-sapling stage areas. The addition of only three species on the mature stage areas also agrees with her findings. The average number of species per census of the three development stages were 12.8, 22.3, and 18.4.

As expected, changes in relative abundance and species composition of the avian community occurred as the age of the stands increased. Figure 2 shows some of the patterns exhibited. In general, the species which were abundant in the first stage decreased as the stands developed and the species which were abundant in the mature stands were infrequent in the seedling-sapling stage. The chestnut-sided warbler, white-throated sparrow, mourning warbler, song sparrow, and yellowthroat were the characteristic species of the seedling-sapling stage. The pole-mature stage was dominated by the ovenbird, red-eyed vireo, least flycatcher, and veery. The intermediate stage had a mixture of the dominant species of both the first and third stages. Qualitative studies by Adams (1908), Stewart and Aldrich (1952), and Beals (1960) reported similar findings.

Winter Birds

Relatively few birds were found in the aspen-birch type in the winter. Six censuses recorded only 14 species (Wunderle and Schemnitz 1969, Goulden 1973, Kienzler 1973, 1974, Park and Goulden 1974, Burgason 1975). The black-capped chickadee and ruffed grouse (Bonasa umbellus) were recorded in all six censuses and the downy (Dendrocopos pubescens) and hairy woodpeckers (D. villosus) were recorded in five censuses. All other species were found only in 1-3 censuses. The black-capped chickadee had the highest density; 23 per 100 acres in one census.

Table 3.--Territorial male birds per 100 acres (40 hectares) of seven censuses of the pole-mature stage.

Species	Stand Location New Brunswick 1/	Minn. 2/	Ontario 3/	Ontario 4/	Ontario 5/	Manitoba 6/	Saskatchewan 7/	Average 8/
Ovenbird	38	22	56	25	20	23	47	33.0
Red-eyed Vireo	11	27	60	10	10	29	51	28.3
Least Flycatcher	5	27	76	32	33	8	15	28.0
Veery	13	16	32	3	4	17		14.2
Swainson's Thrush	7	5	2	10	6	6		6.0
Black and White Warbler		5	12	4	1	14		7.2
American Redstart	11			2	2	80		23.8
Mourning Warbler		11	10	10	10			10.3
Chestnut-Sided Warbler		22		2	4	1		7.3
Rose-breasted Grosbeak	5	11	8			3	2	5.8
White-throated Sparrow	4	5		6	8			5.8
Hermit Thrush	2	11	4					
Magnolia Warbler	2	5			1			
Canada Warbler		22	4			5		
Black-trhoated Green Warbler		5	16				15	
Winter Wren		5		2	4			
Ruffed Grouse			4	2	2			
Philadelphia Vireo				21	25	9		
Bay-breasted Warbler				2	2		5	
Red-breasted Nuthatch	4	11						
Blackburnian Warbler		5	12					
Purple Finch		5	4					
Downy Woodpecker		5				1		
Great Crested Flycatcher			12			5		
Woodcock				2	1			
Tennessee Warbler						2	10	
Others	16	46	52	0	3	7	11	
Total Density	132	282	366	138	143	211	156	204.0

1/Thirty-forty year old aspen birch stand, Erskine 1969.

2/Thirty-forty year old paper birch-red maple stand, Doran and Todd 1976.

3/Mature aspen-birch forest, Price and Speirs 1971.

4/Mature poplar forest, Erskine 1970.

5/Mature poplar forest, Erskine 1971.

6/Mature aspen-birch forest, Erskine 1972.

7/Mature birch-aspen forest, Erskine 1973b.

8/The average was calculated only if a species occurred in four or more censuses.

Table 4.--Bird species diversity values (BSD) and total number of species recorded for [illegible] categories of stand development.

Stage of Development	BSD1/	Total Number of Species	Source
Seedling-sapling Stage			
1 year old clearcut	1.90	8	Niemi 1974b.
2 year old clearcut	2.03	11	Niemi 1975.
2 year old burn	1.94	9	Bergstedt 1973.
2 year old burn	2.16	16	Bergstedt and Niemi 1974.
3 year old burn	2.26	18	Niemi 1974a.
10-15 year old clearcut	2.50	15	Doran and Todd 1976.
Sapling-pole Stage			
21 year old stand	2.71	17	Townsend 1968.
Pole stage stand	2.22	14	Clink 1969.
Pole stage stand	3.29	36	Breault and Farrar 1972.
Pole stage stand	3.07	35	Farrar 1973.
Approx. 30 year old stand	1.64	10	Erskine 1973a.
Pole-mature Stage			
30-40 year old stand	2.32	14	Erskine 1969.
30-40 year old stand	3.12	28	Doran and Todd 1976.
Mature stand	2.61	26	Price and Speirs 1971.
Mature stand	2.30	16	Erskine 1970.
Mature stand	2.41	19	Erskine 1971.
Mature stand	2.08	15	Erskine 1972.
Mature stand	1.79	11	Erskine 1973b.

1/Calculated from the Shannon information formula, BSD = $H' = -\Sigma p_i \ln p_i$, where p_i = the proportion of species (i) of all birds in a census (MacArthur and MacArthur 1961).

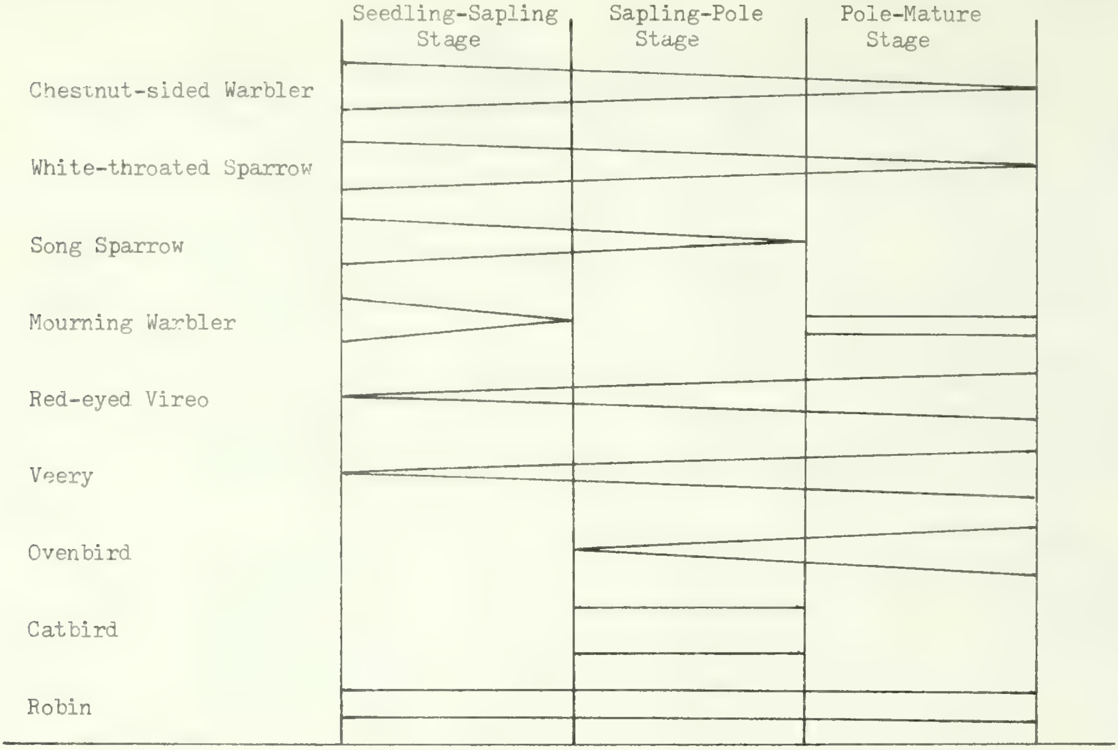

Figure 2.--Changes in species relative abundance in relation to ecological stand age.

MANAGEMENT GUIDELINES

The recent movement to develop management guidelines for nongame species has emphasized the concept of community management versus the traditional single species concept. This emphasis is to be lauded. However, a species exists only where the habitat provides its specific requirements. Some species have a wide range of tolerance for specific factors (eurytopic species) while others have a restricted range of tolerance (stenotopic species). It is necessary that the stenotopic species and their specific requirements be identified before the management prescriptions are formulated. Trade-offs in species diversity may be necessary to prevent the loss of stenotopic species.

It is obvious from the 18 censuses summarized in Tables 1-3 that only 16 of the 78 species recorded were abundant in one or more stages of stand development. Of the remaining 62 species, there are probably some for which the aspen-birch type in any form would be marginal habitat. Yellow-rumped (Dendroica coronata) and blackburnian warblers are examples of this category. They appear in low density in the aspen-birch type when coniferous species are present in the understory or canopy, but they are considered members of the spruce-fir avian community. For other species, presence of some special factor can be the difference between abundance and scarcity or even absence. Balda (1975) found the abundance and diversity of cavity nesting birds increased with increased availability of snags. The house wren apparently responded to the availability of cavities in snags on one census area (Bergstedt and Niemi 1974). Erskine (1972) was of the opinion that the dense deciduous understory was a factor in the extremely high density of redstarts in one Manitoba census. Other factors may have been responsible for high densities of yellow warblers (Dendorica petechia) and indigo buntings on one census area (Townsend 1968) as they were infrequent on the other census areas. Until the specific requirements for all species are identified, only basic guidelines of management can be formulated.

Maintenance of the aspen-birch type requires even-aged management in the form of seedtree or clearcutting prescriptions. In areas where a pulpwood market exists, avian management and pulpwood management are compatible. The stands should be cut on a 40-60 year rotation, depending on site quality. The loss of vigor of parent trees after age 60 reduces their suckering and stump sprouting ability (Folwells 1965), resulting in possible type conversion to tolerant hardwoods or conifers. Slash removal is not necessary in a commercial cutting and may not be desirable for avian management. The larvae and adults of wood-boring beetles that attack slash are fed upon by several species of woodpeckers (Martin, Zim, and Nelson 1961, Conner and Crawford 1974). Prescribed burning of the felled timber can be used to regenerate the type where commercial outlets are not available. However, aspen fuels need to be cured before they can sustain a hot fire (Perala 1972).

The optimum size of the cuttings has not been determined. The minimum size of 10-20 acres needed to make pulpwood operations economically feasible is probably compatible with avian management. Shape of the cut should be considered for areas over 50 acres to provide a high ratio of edge to area. Rectangular strips or irregular shaped cuts create more edge than square cuts.

Several practices can be used to increase species diversity of an area. Cuttings should be spaced temporally to create several age classes on a management unit. Cuttings at 10-15 year intervals with a 40-60 year rotation would result in four age classes. The spacial arrangement of the cuttings should also be considered. "Snag management" as previously mentioned, can increase diversity. Special habitats within a stand (e.g. riparian vegetation) should also be maintained if maximum species diversity is an objective. These additional practices may reduce pulpwood yields or require some additional expenses.

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OAK FOREST BIRD COMMUNITIES

John R. Probst[1]

Abstract.--Oak forests represent the largest forest type in the United States. The density and diversity of avian species in oak forests are dependent on habitat factors such as vegetation structure and successional stage. Therefore, they are greatly affected by management considerations such as cutting, thinning, rotation age, stand size, and tree species composition. The species number and population sizes of breeding birds and winter birds are contrasted.

The Appalachian Oak and/or Oak-Hickory types form the largest forest type in the United States, representing about 125 million acres. Eastern hardwoods compose more than half the commerical timber land in the United States, and the Oak and Oak-Pine types combined total about 147 million acres, or 60 percent of the eastern commercial forest. This acreage exceeds the total commercial timber area of all western forest types combined (U.S. Department of Agriculture, Forest Service 1977). Because this forest type spans a wide range of altitudes, latitudes, and longitudes, a number of bird species are associated with it as breeding, migrant, or wintering birds. In the nesting season, from 90 to 100 different bird species can be found in northeast or north-central oak forests, clearcuts, and edges. The avifauna of southern Oak-Hickory and Oak-Pine forests has been covered by Evans (1978).

DESCRIPTION AND EXTENT OF THE TYPE

The oak forests of the northeast and north-central United States are more concentrated in the northern Appalachian region, extending north to New York and southeastern New England, and west to Ohio and the Cumberland Plateau. Oak forests are common in the Piedmont of the Mid-Atlantic States, and the oak-hickory type forms a mosaic with other vegetation types in much of Ohio, Indiana, Illinois, and southern Michigan. In addition, oak stands are found at the border of the northern hardwoods region in Minnesota, Wisconsin, and Michigan, and oaks can be the major seral species in both the mixed mesophytic area and the northern hardwoods type. Last, oaks are the major tree species in the prairie borders (Minnesota, Wisconsin, Illinois, and Iowa) in oak savannas or in fairly closed stands that expand and contract with temporary climatic conditions and fire.

Oak Forest Acreages for Selected States (U.S. Department of Agriculture, Forest Service 1977)

		(millions of acres)
1.	Missouri	11.46
2.	Virginia	10.33
3.	Tennessee	9.71
4.	Kentucky	9.27
5.	Pennsylvania	7.98
6.	West Virginia	7.50
7.	North Carolina	6.36
8.	Ohio	3.00
9.	Wisconsin	2.76
10.	Indiana	2.42
11.	Illinois	2.26
12.	Michigan	2.12
13.	Maryland	1.45
14.	Connecticut	1.39
15.	New York	1.36
16.	Minnesota	1.33
17.	Massachusetts	1.26
18.	Iowa	1.25
19.	New Jersey	.81
20.	New Hampshire	.62
21.	Maine	.29
22.	Vermont	.11
23.	Delaware	.08

The most common oak species are northern red *(Quercus rubra)*, white *(Q. alba)*, black *(Q. velutina)*, scarlet *(Q. coccinea)*, and chestnut *(Q. prinus)*. On medium sites hickories, such as pignut *(Carya glabra)* or mockernut *(C. tomentosa)*, may form a minor part of the canopy, and on moist sites yellow-poplar *(Liriodendron tulipifera)*, shagbark hickory *(C. ovata)*, and various northern hardwood species may be present. On steep slopes and ridge tops, pitch pine *(Pinus rigida)* may occur regularly as a minor component. Red maple *(Acer rubrum)* and white ash *(Fraxinus*

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mericana) usually fill in openings in the anopy and can often be major constituents of he canopy or understory. Such openings can esult from natural causes, or be caused by elective cuttings, or thinning.

In southern Michigan, northern pin oak *Q. ellipsoidalis)* can be important, and bur oak *Q. macrocarpa)* can be dominant in southern innesota and the prairie borders. Oak forests n southern New England may be heavily mixed ith white pine *(P. strobus)* as well as beech *Fagus grandifolia)* and maple.

Tree species of oak forests that are sually of subordinate status include flowering logwood *(Cornus florida)*, sassafras *(Sassafras lbidum)*, black birch *(Betula lenta)*, and black um *(Nyssa sylvatica)*. Choke cherry *(Prunus irginiana)*, hop hornbeam *(Ostrya virginiana)*, lack cherry *(P. serotina)*, and redbud *(Circis anadensis)* are less common on the poorer sites. he shrub layer of the drier sites is usually lominated by ericaceous shrubs such as laurel, lueberries, huckleberries, and sweet fern *Myrica asplenifolia)*. Fair sites may have itch hazel *(Hamamelis virginiana)*, azaleas, arious ferns, club mosses, and striped maple *Acer pensylvanicum)*. The better oak stands may ontain such plants as green briars, viburnums, oison ivy *(Rhus radicans)*, and spicebush *Lindera benzoin)*.

The most distinguishing characteristic bout the herb layer in oak forests is its poor levelopment. Tree seedlings and blueberries ften form the predominant forest floor cover, ut common herbs are wild sarsaparilla *(Aralia udicaulis)*, may apple *(Podophyllum peltatum)*, eaberry *(Gaultheria procumbens)*, asters, loodroot *(Sanguinaria canadensis)*, and rilliums.

Major tree species in old-field succession n the oak forest region include hawthorne, spens, black locust *(Robinia pseudo-acacia)*, ed maple, black cherry, and choke cherry. In ak barrens that result from fire, scrub oak *Q. ilicifolia)* may form nearly pure, almost impenetrable stands. In more mesic situations, shrubs such as dogwood may be the earliest oody pioneers and may be associated with merican elm *(Ulmus americana)* and black walnut *Juglans nigra)* along with the more mesic oak species. On dry sites such as slopes or bandoned upland pastures, conifers such as red edar *(Juniperus virginiana)*, pitch pine, and scrub pine *(Pinus virginiana)* are well represented. The oaks themselves tend to seed in rom the edges and are rarely pioneers in bandoned fields because the acorns need to be spread by animals for longer dispersal distances.

The oak type grades into the oak-pine type in drier situations and into mixed hardwoods (mixed mesophytic) in moister areas. Intermediate stands on mesic sites contain greater proportions of red oak, yellow poplar, American basswood *(Tilia americana)*, beech, sugar maple *(Acer saccharum)*, white ash, and hickories. Compared with other hardwood forest types, oak woodlands typically have simple vegetation structure and often contain few plant species.

BREEDING BIRD COMMUNITIES

Species Composition

(Blue Jays and Brown-headed Cowbirds are species of generalized habitat requirements that are found in almost every stand, regardless of age or structure.) However, most birds require a specific type of habitat. The breeding bird species of oak forests can be conveniently grouped into five categories, each of which responds to a different habitat (table 1).

(1) The bark foragers nest in cavities of dead or dying trees, and drill, chip, or glean for their food on the tree trunks or large branches. Many other secondary cavity-nesting birds are ultimately dependent on those bark foragers that excavate cavities. Some examples of birds in this group are Flicker, White-breasted Nuthatch, Downy Woodpecker, and Hairy Woodpecker.

(2) The active gleaners that feed in the tree canopy. Some examples of birds in this group are Chickadee, Tufted Titmouse, and Red-eyed Vireo.

(3) The pursuers also feed in the tree canopy but follow a sit-and-wait strategy. Flycatchers and tanagers are the common pursuers in oak forests.

(4) The ground species are associated with the shrub and sapling layers, but not all members of this group use the understory for their feeding activities--Thrushes, Rufous-sided Towhees and Ovenbirds forage on the ground and use the shrubs for cover and nest sites.

(5) Warblers are the main species associated with a dense growth of saplings and small trees beneath the canopy. Other birds, such as Parids, can become more abundant under these conditions than they would be in forests with a tree layer of simple structure. Because most Appalachian Oak forests are too dry and open for a dense, continuous column of foliage to develop, woodland warblers are less common than they are in more mesic forest types, such as

Table 1.--*Consuming biomass of the forest feeding groups (adapted from Probst 1976)*

(In grams per 40 hectares)

Plot No.	Bark	Gleaners	Pursuers	Ground	Warblers	Misc.	Total
Young-1	--	219	178	1,321	44	459	1,762
Young-2	--	553	100	602	--	403	1,255
Intermed.-1		432	583	10	--	403	1,600
Intermed.-2	556	273	618	360	--	457	1,807
Intermed.-3	771	910	452	--	--	476	2,133
Mature-1	940	320	450	--	--	403	1,710
Mature-2	637	160	716	--	--	678	1,513
Mature-3	1,124	384	446	--	--	364	1,954
Mature-4	956	264	864	66	--	663	2,150
Complex Can.	340	569	883	2,702	--	221	4,494
Complex Can.	454	770	375	939	--	559	2,538
Forest-32	1,150	224	713	1,446	--	301	3,533
Forest-33	839	629	963	1,387	--	325	3,818
Forest-34	673	751	342	361	--	476	2,128
Forest-35	521	164	676	1,354	--	831	2,715
Forest-36	388	236	545	1,453	95	442	2,717
Forest-37	41	634	473	1,304	216	--	2,668
Forest-38	621	251	700	1,407	161	658	3,140
Forest-39	418	568	308	2,143	470	400	3,907
Average	579	437	547	887	52	448	2,502

Mixed Hardwoods. When present, Black-throated Green Warbler, Black and White Warbler, and Chestnut-sided Warbler are the most regular species, but in the southern parts of the oak forest region, Hooded Warbler, Kentucky Warbler, and Yellow-throated Warbler can be important in stands of suitable vegetation structure.

There is a group of species that favors open, mature stands with large, spreading tree crowns. Such conditions are most common in floodplain forests, but can also occur in other forests with incomplete timber harvesting or heavy natural tree mortality. In forests of this structure Yellow-throated Vireos, Blue-gray Gnatcatchers, and rarely, Cerulean Warblers may be found.

As a young oak forest matures, the relative importance of the avian groups discussed above changes. Shrub cover diminishes with canopy closure and eliminates some ground feeders and foliage gleaners that require dense growth. The maturation of the tree layer makes possible the availability of the bark-foraging niches, and the openings in the canopy can be used by pursuers. If management or historical factors such as fire or disease allow for an understory and complex canopy to develop, ground feeders will be common and warblers and other foliage gleaners should also be present. However, the lower age distribution of trees in such stands are less favorable for bark-foragers than forests with more large trees.

Breeding bird censuses conducted in 16 upland oak forests with widely different structures showed that the following bird species occur in most types of forests (adapted from Probst 1976):

Species	*Frequency* (percent)
Red-eyed Vireo	100
Downy Woodpecker	93
Scarlet Tanager	93
Cowbird	93
Wood Pewee	87
Crested Flycatcher	87
Blue Jay	80
Flicker	80
White-breasted Nuthatch	80
Parid	67
Additional Bark Feeder	40

The first nine species occurred in at least 80 percent of the stands examined. The most frequent additions or substitutions to the basic census were Parids and additional bark feeders. This indicates that forest bird communities are formed by an accumulation of rarer species combined with this more constant group.

The bird species of open habitats in the oak forest region are similar to those in many other forest types. Species of young seres tend to be widespread, and many are found in several biomes. Such wide distributions are rare among climax bird species (Pitelka 1941) This pattern may be a result of the scarcity of secondary habitats. As succession progresse the loss of grasses and forbs decreases the opportunities for seed- and plant-eating birds, while the addition of shrubs and trees provides new niches for primarily insectivorous species.

The red-winged Blackbird and Field Sparrow re overwhelming dominants in the open fields nd shrublands, respectively. These two species ypically have densities exceeding those for all ther species in the community combined. Other mportant open-field species are Eastern Meadowarks and Grasshopper Sparrows. In the shrubands, subdominant species include the ellowthroat, Rufous-sided Towhee, Indigo Buntng, Goldfinch, Song Sparrow, Chipping Sparrow, nd Golden-winged Warbler.

Avian Diversity and Density

At the level of the forest stand, avian iversity is strongly influenced by the vertical omplexity of the vegetation (Karr and Roth 971, MacArthur and MacArthur 1961, Probst 1976, illson 1974) and the amount of patchiness or orizontal heterogeneity (Balda 1975, Roth 1976). he number of species increases with the size f the area sampled, but levels off rapidly in niform stands. The number of bird species learly increases with the number of habitat ypes, a factor strongly affected by climate nd topography. The turnover in species per nit of habitat change is also an important actor. All of the above are determinants of the vian diversity of a region or large group of anagement units.

The following discussion of avian density nd diversity is based on census data published n *AMERICAN BIRDS* and on data from a study I onducted in Central Pennsylvania (Probst 1976). he Pennsylvania information was obtained at 9 study plots--7 fields or grasslands, 6 shrubands or old fields, 1 open shrub thicket, 6 learcut or regeneration stands, and 19 forest tands.

The number of breeding birds in oak forest ensus plots ranges from 9 to 29 species. The stimated number of territorial males per 40 ha anges from 65 to 390. The average values for 6 oak census plots are 21.2 species and 222 ales/40 ha. Mesic stands can have higher opulations; mixed hardwood stands range as igh as 413/40 ha (average = 247) with a maxium of 66 species (average = 26.3). Density nd diversity of breeding birds generally ncreases with plant succession (Johnston and dum 1956, Shugart and James 1973, Shugart *et al.* 975). Consequently, it is often possible to redict avian density and diversity from stimates of total plant cover (Karr and Roth 971, Willson 1974, Probst 1976). However, at east in the oak forest region, young seres may verlap with forest stands in their values for vian density and diversity (tables 2 and 3). or example, the densities of birds in shrublands nd clearcuts are usually higher than those of ry upland forests.

Table 2.--*Avian diversity of oak forest seres*

Habitat-group	Plots	Equally common species[1]	Species	Equatability[2]
		- - - - - *Number* - - - - -		
Field	7	3.7-4.5	5-8	0.46-0.75
Shrub				
Open	1	6.3	9	.70
Woods	2	2.6-2.9	3	.87-.92
Simple canopy (narrow age range)				
Young	2	5.6	7	.80
Intermediate	3	6.5-8.8	8-11	.72-.81
Mature	4	7.6-9.1	9-11	.73-.85
Complex canopy (wide age range)	2	7.4-9.3	13	.57-.71
Complex forest (multi-layered)	8	7.7-15.0	11-20	.59-.92
Shrubland	6	5.2-11.6	9-18	.48-.81
Clearcut	4	8.7-11.2	14-16	.60-.75

[1] Calculated as $2^{-\Sigma p_i \log_2 p_i}$, where p_i is the proportion of each species.

[2] Number of equally common species divided by the actual number of species.

Table 3.--*Avian abundance of oak forest seres*

Habitat-group	Plots	Birds per 40 ha	Mean abundance per species
		- - - - *Number*	- - - -
Field	7	54-80	9.1-14.3
Shrub			
Open	1	181	20.1
Woods	2	59-66	20-22
Simple canopy (narrow age range)			
Young	2	37-52	5.3-7.4
Intermediate	3	65-106	5.9-11.8
Mature	4	72-89	6.5-8.9
Complex canopy (wide age range)	2	131-156	10.1-12.0
Complex forest (multi-layered)	8	102-188	7.8-12.9
Shrubland	6	132-270	8.9-15.9
Clearcut	4	296-349	20.8-23.3

Predictions of bird species diversity by total coverage show a leveling off somewhere in the high range of values characteristic of forested habitats, so estimators that account for the distribution of foliage are often used. MacArthur and MacArthur (1961) found that Bird Species Diversity (BSD) for a broad range of habitats could be predicted from a measure called Foliage Height Diversity (FHD), an average of the logarithms of the *proportions* of foliage in three height intervals. Although this method underlines the importance of habitat complexity to avian diversity, it has a number of faults (Probst 1976). In addition to being an unnecessary abstraction, the FHD predictor does not allow for differential contributions by the natural layers (structural forms) to the vegetation, especially in plots with a single layer or life form. It also does not account for the absolute amount of foliage in a layer or the total of all layers, and does not register site variations in productivity. As a result, this predictor lacks generality and often cannot be used to compare habitat types as broad as all forest stands within a locality (Probst 1976, Willson 1974). It is more informative to examine the differential contribution of the herb, shrub, and tree layers to avian diversity (tables 2 and 3). When this is done, it can be seen that fields (grasslands) have from 5 to 8 species, but the mature tree layer (simple canopy) in oak forests has from 9 to 11 species. An open scrub oak barren with little herb cover approximates a shrub monolayer and has an intermediate number (9) of species. Thus, the fields show the lowest bird diversity of all habitat groups and simple forests have diversities in the range of more complex open habitats. Complex forests have a higher average diversity than simple canopies, and clearcuts have a slightly higher average than shrublands.

Each layer or structural form of the forest adds to avian diversity, and the amount of cover of each layer also adds to the number of species up to a certain plateau after which the number of bird species remains constant. However, differences in bird diversity are best predicted using only shrub and sapling cover, because in most practical field situations the herb and tree layers are already in the plateau region.

Ground-feeders, shrub-foragers, and bark-foragers can be estimated by shrub-sapling cover. However, it is difficult to predict the density or biomass of the canopy birds by either plant coverage, volume, or conic surface estimates (Probst 1976, Willson 1974). Tree conic surface is linearly related to bark surface area and leaf surface area (Whittaker and Woodwell 1967) and has the potential for simultaneously predicting both bark-feeders and canopy insectivores.

Much of the constancy in the avian density and diversity of the forest canopy can be explained by compensatory changes in the composition of the forest avifauna with changes in age or structure of woodlands. Substantial changes in composition usually do not significantly alter the total species count (fig. 1). Major changes in composition occur when a forest matures (loss of ground species, addition of bark-feeders), when shrubs are added (addition of ground birds), and when a simple forest is contrasted with a complex forest (addition of warblers and thrushes, and the eventual loss of a pursuer and some bark species). In forest stands, great changes in structure cause predictable alternations in avian composition but surprisingly small differences in bird diversity.

Winter Birds of Oak Forests

A large portion of the summer avifauna of the oak forest region migrates to the southern United States or Central and South America in winter. Christmas Bird Counts conducted on a standard 458 km^2 area commonly show land bird counts of from 8 to 14 species (Tramer 1974).

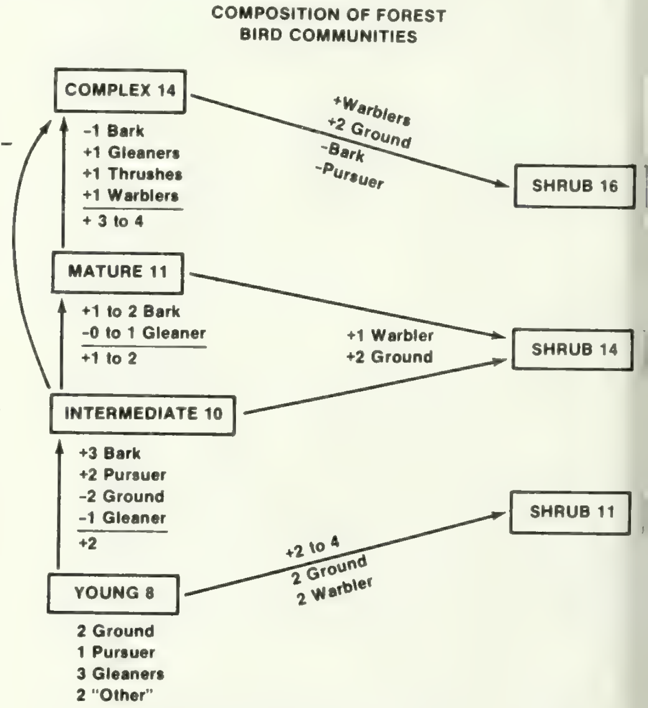

Figure 1.--*Vegetation changes alter the importance of various bird feeding groups, but these changes are often offsetting. The presence of shrubs has a significant positive effect on total species number. The same may be true to a lesser extent for added canopy complexity. The third net increase involves the maturation of the canopy.*

The average number of bird species found n oak forests in the winter is 9 (Winter Bird opulation Studies, *AMERICAN BIRDS*). The number f species ranges from 3 or 4 to 16 (Probst and earson, unpublished). The average number of pecies from these winter counts represents ess than half of those for oak breeding bird ensuses. The number of individuals per 40 ha or the winter counts ranges from 8 (Minnesota) o 140 (Virginia) with an average of 69.4. This s less than a third of the density for breedng bird censuses in the same forest type. By ontrast, bottomland hardwoods in Louisiana may ave twice as many birds in winter as are preent in the summer (Dickson 1978).

Obviously, the oak forest winter avifauna s limited directly or indirectly by climate. evere temperatures place heavy energy demands n birds at a time when food and cover is inimal. Continuous snow cover eliminates ost ground-feeding species such as Common rackles, Carolina Wrens, and many finches, hich are numerous in the southeastern United tates during the winter. Insectivores, such s vireos and warblers, also winter south of ost of the oak forests. The Yellow-rumped arbler is usually the only winter warbler to e found in the regions where oak forests are he dominant forest type.

The insectivores that are year-round resients such as Parids or Woodpeckers specialize n arthropods that have over-wintering forms in he crevices of bark or branches. It has been uggested that mixed hardwood-conifer forests ay provide better winter habitat for birds Evans 1978). Few tree species in oak forests etain usable seeds in the winter, as do the irches and conifers of the Northern Hardwood orests. Consequently, stands that contain ine or hardwoods such as yellow poplar or hite ash may have higher winter bird populaions than pure oak stands.

Bird species that forage in shrubs or on he ground are often found in edges, old fields, r forest openings during the winter because hese habitats provide more cover and food seed-bearing grasses and herbs and fruit-earing shrubs). In old fields where conifers re important seral species, bird populations ight be higher but data are scarce. Winter ird populations may be augmented by irregular nvasions of northern finches (crossbills, rosbeaks, and redpolls) in some years. Because ost of these species are normally found in oreal or mixed coniferous forests, when found n oak forests they are usually in stands with ome mix of conifers or seed-bearing hardwoods.

For almost all bird species, populations re generally higher in valleys or lowlands than n ridges and mountains. This is even true or high elevation stands with a good conifer omponent. The low density of winter bird populations in highlands is probably related to the short growing season, low productivity, and rigorous winter climate of the highlands.

The most regular or abundant winter bird species of oak forests are the Black-capped Chickadee, White-breasted Nuthatch, Dark-eyed Junco, Golden-crowned Kinglet, Downy and Hairy Woodpeckers, Common Crow, Blue Jay, and Brown Creeper. In the southern part of the region, Carolina Chickadees, Tufted Titmice, Red-bellied Woodpeckers, and Carolina Wrens can be an important part of the winter avifauna.

TIMBER MANAGEMENT

Although timber management practices in oak forests vary with geography, site, and species composition, some common strategies apply (Sander 1977, Trimble 1973, Watt *et al.* 1973). Even-aged management through clearcut harvesting is the usual practice. However, because planting oaks is rarely practical, a shelterwood is often used if advance regeneration or anticipated sprout growth is insufficient. Uneven management by group selection can regenerate oaks but is less economical and is difficult to administer and manage.

Species composition and desired products of oak forests vary with site quality. The best sites (site index > 75) are usually managed for saw logs or veneer logs, and fair sites (site index 55-75) are managed for saw logs or pulpwood. If poor sites (site index < 55) have commercial potential, they are managed for pulp. Because the mix of species in oak stands depends on ecological conditions, and regenerated stands come from sprout growth and advance regeneration, species composition goals usually closely follow the natural tendencies. The associated species on the better sites in the northern part of the oak range include sugar maple, white ash, basswood, and black cherry. In the south-central States, yellow-poplar and black walnut can be important, and hickories are common in the southwest part of the oak region. On average sites in the north, white and red pine are found with the hardwoods, and farther south hickories and shortleaf pine are characteristic. On poor sites, jack pine and aspen are common in the north-central States. These marginal stands are managed for pulpwood, wildlife, or converted to conifers such as jack pine or shortleaf pine. If conversion is not prescribed, management is usually minimal. Fair sites are ideal for oaks and are managed for oaks or an oak-hardwood mixture. The lower part of this range of sites is often managed for oak-pine. In stands of intermediate quality, commercial thinning becomes possible. If there is to be only one thinning, it should be done at about 30-40 years because after that time the released trees will not respond well.

On better sites oak forests are managed for oak-hardwoods or converted to pure hardwoods through natural succession of the advance reproduction. This process may be accelerated by spraying oak sprout-growth. Oak-hardwood stands may be thinned to 60 percent of stocking as often as every 10 years up until 3/4 of rotation age. Best results are obtained by thinning intermediate trees from below to release the more vigorous, dominant trees.

Rotation age varies with site and desired product. Forests managed for sawtimber have rotation ages of 60 to 120 years, and forests managed for pulp have rotation ages of 40-60 years. But rotation age can be shortened by appropriate thinnings.

The stand size of oak forests may vary according to physical, economical, or silvicultural considerations. The lower limit to stand size is fixed by efficiency of harvesting and the need for the intolerant oaks to be released from the influence of nearby mature trees. In addition, animal browse activity can be more severe in small plots. As a result, stands are usually not less than 2-5 acres. The upper limit is about 100 acres and is often determined by topography and the age distribution of the management unit. Concerns about soil erosion, water quality and quantity, and nutrient losses and factors such as wildlife habitat diversity and aesthetics all tend to keep stand size down. Also, very large stands are difficult to work into an acceptable rotation schedule.

MANAGEMENT IMPACTS ON AVIAN COMMUNITIES AND SUGGESTED GUIDELINES

The effects of timber harvesting on avian populations varies during the life of the regenerating stand. Clearcutting and shelterwood regeneration usually cause a drastic reduction in the avian community population size and an almost complete turnover in species composition the first growing season after harvest. However, vigorous sprout growth often results in second-year populations higher than those of mature stands. Peak density and diversity of birds probably occurs 5 or 6 years after cutting on most sites, though peaks might be reached later in understocked stands. When regenerating stands shade out the shrub layer, the density and diversity of birds is reduced. Open, less productive woodlands may be more favorable to a wider range of species at this stage due to greater foliage stratification. Avian communities similar to those of mature forests generally develop when the dominant and codominant trees reach 40 to 50 feet in height. At that point, bark foragers are well-established and ground-feeding birds have reappeared. If the loss of undergrowth in regenerating stands is marked, species such as Wood Thrushes and Rufous-sided Towhees can show a bimodal distribution, with peaks in the mature forest and late clearcuts.

The principal difference between clearcut and shelterwood harvests is in the reduced populations of bird species in the residual trees of the latter. Other species found in shelterwoods, such as Northern Orioles or Blue-gray Gnatcatchers, may be absent from any other stage of oak forest development. If small residual trees are left during harvesting operations, they may provide sufficient habitat diversity to allow some foraging by birds from surrounding forest areas, or to allow earlier invasion by species with a preference for elevated song perches (Alder Flycatcher, Golden-winged Warbler, etc.). Another habitat factor that can operate under the shelterwood system is a higher probability of associated shrub species gaining temporary dominance over oak sprouts and seedlings during the younger years of the stand. This tends to favor ground-feeders over the smaller finches and warblers.

Thinning Practices

Thinnings open the canopy and make it less useful for insectivores but create better opportunities for flycatchers and other pursuers. As thinned stands mature, the dominants may develop fuller crowns, which are favorable to several bird species that are scarce or uncommon in oak forests. If the thinning substantially releases the undergrowth, bird species using those layers will be enhanced. Conversely, those species will be eliminated if the underbrush is removed to stimulate tree growth or as part of a "whole tree" chipping operation. This results in a larger proportional decrease in avian biomass in oak forests than in other forest types where species of the upper strata are usually more dominant (table 1). In addition, understory removal may not even be justified by its contribution to tree growth (Dale 1975).

Rotation Age

The major impact of adjusting rotation age will be on the bark foragers, and primary and secondary cavity nesters. Rotation age should be long enough to allow a sufficient number of trees to die for the cavity excavators to utilize and to optimize the foraging substrates for birds that search for prey on tree bark surfaces. In addition, dead trees of all sizes are used as song perches by many birds, and some species also favor snags as perches from which to hawk or sally after prey. When forests are harvested, enough snags should be saved to accommodate the projected number of cavity nesters at the different stages of regeneration, while allowing for the expected attrition of snags during the rotation period. The species, size, and condition of trees preferred by each species of woodpecker needs further research (Conner 1978).

Another benefit to nongame birds from long ations is the increased populations of ds--chiefly warblers--that select forests h more stratified foliage. Consequently, e portion of the stands in a management unit uld be left as old growth. In stands of rter rotation, it may be necessary to create ificial snags (Conner 1978).

Single Species Management

Bird species requiring young growth are commodated by normal timber harvesting. This aves a small number of species with more ecialized or unusual requirements that may quire specific management prescriptions. ever, the land manager can do little to ance species that are rare in an area ause their distributions are centered in ther forest type or geographical region, nor he manage for species that have population e depressed by factors that are not habitat ated. The problem of maximizing the popu- tions of the more common species is a second- ler concern, and is complicated not only by lack of specific knowledge of each species also by the virtual certainty that such escriptions would contradict or conflict h one another. Although optimization of roup of individual species populations ng all stands is easily handled by modern hods, it will always be difficult to assign ative values to the more common bird species.

Stand Size

A very general account of species number area relations was given above. When avian sus results are broken down into subplots, species count is usually complete after ut 5 ha (fig. 2). However, this includes e partial territories in census plots that a portion of a larger, forested area. le most of the smaller songbirds have home ges of less than 5 acres, very few species all of the suitable habitat available to m. Most bird species show very patchy tributions so rare species usually result e from fragmentation than dilution. The sity of a particular avian population is ely related simply to the census area ided by the average home range size.

The ideal stand size is probably about 10 20 acres and would accommodate several ividuals of the both common and uncommon cies. Stands that are too large tend to rease overall habitat diversification. ds with large home ranges can almost always several proximate large patches of habitat, a variety of habitat types.

Tree Species Composition

Tree species composition of eastern decid- s forests has little effect on bird communities because most birds select habitats by vegetation structure rather than by the tree species or genera that compose the forest. Any avifaunal differences between oak stands and mixed hardwood stands with greater plant variety are almost certainly due to differences in productivity and/or vegetation structure. However, forests containing appreciable densities of trees bearing usable seeds could receive more winter use by birds in some years, but there is no conclusive data to support this idea. Another question that needs further research is the possibility that trees with smooth bark surfaces such as aspen may contain fewer arthropods than those with rough bark. If so, bark foragers could be less prevalent in forests stocked with smooth-textured tree surfaces.

The management practice with the most potential to severely affect bird communities is conversion of hardwood stands to conifer plantations. Oak stands on poorer sites are often converted to red, jack, or shortleaf pine. Although such plantations may have higher winter bird densities, they would support a much lower density and diversity of breeding birds due to their extreme structural simplicity and scarcity of dead trees. In addition, undergrowth may be virtually eliminated for most stages of the rotation by site preparation, release, and shading.

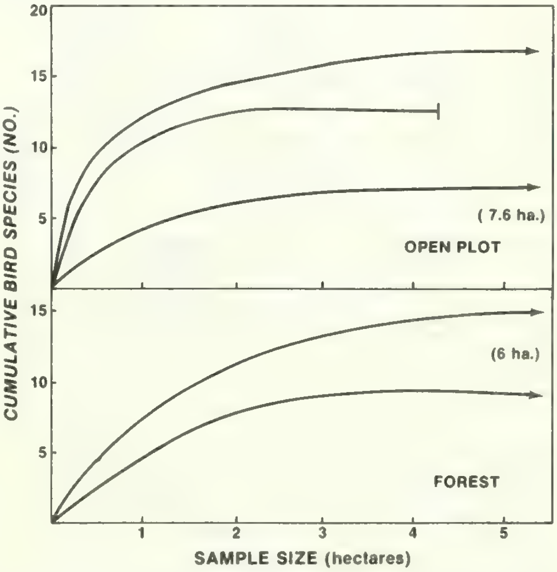

Figure 2.--*Species-area curves for open and forest study areas, which plot cumulative bird species vs. size of plot subset for selected plots of contrasting diversity. All plots show a plateau before 4 ha size. The minimum plot size was 4 ha and most were 6 ha or more. This would indicate that sampling sufficiency for species number has been achieved. The three truncated curves (indicated by arrows) show no increase in cumulative species through their full areas of 6 ha for the forest and 7.6 ha for the open plot.*

In summary, the density and diversity of breeding birds in oak forests can be enhanced by practices that increase the rotation age, structural complexity, and the variety of stands. Some mixture of conifers in some forests benefits both the breeding and winter avifauna, but conversion to pine plantations is detrimental to many breeding populations.

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Wednesday, January 24

NONGAME BIRD HABITAT MANAGEMENT

Moderator: Ruth L. Hine
Wisconsin Department of
Natural Resources

MANAGEMENT OF NORTHEASTERN PINE FORESTS FOR NONGAME BIRDS

David E. Capen[1]

Abstract.--Forests of white, red, jack, and pitch pine may be managed to provide productive habitat for nongame birds. Diverse avian communities often inhabit stands of pine, but few species are restricted to pine forests. Single-species and multi-species wildlife management philosophies are discussed and are related to four principles of managing forest habitat for nongame birds. Even-aged silviculture is recognized as the predominant harvesting practice in pine forests. Forest management which promotes natural regeneration, hardwood understories, and old-growth stands is recommended to enhance habitat for birds. The endangered Kirtland's warbler nests only in young stands of jack pine and is a reminder that pine forests should not be overlooked as wildlife habitat.

INTRODUCTION

Wildlife managers often regard pine forests as "biological deserts" (Castles 1974). Indeed, an intensively managed pine forest may represent a structurally "sterile" habitat for birds (Wiens 1978), and there is a resulting tendency to ignore nongame bird populations in pine forests. Shugart et al. (1978) cautioned that a disregard for bird communities of pine forests could create future shortages in critical habitat for some species. The endangered status of the Kirtland's warbler, which occurs only in stands of jack pine, serves to remind us of this point. Intensive timber management may effectively create biological deserts where extensive stands of pine forests occur; alternatively pine stands may be managed to provide productive habitats for birds.

The objectives of this paper were (1) to review the silvics and management of pine forest types which occur in the northeastern and north central states; (2) to describe the bird communities associated with pine forest types; and (3) to propose management considerations and practices which will allow pine forests to be managed as productive habitat for nongame birds. I have suggested management alternatives which favor nongame birds, and have ignored, within reason, other demands upon the resources of forests. It will be the function of this paper, then, to provide recommendations which will allow optimum benefits for nongame birds in pine forest habitats. Hereafter, wildlife biologists involved in natural resource decision-making processes may be better prepared to propose management compromises which will benefit the nongame resource

Scientific names of all animals and plants mentioned in this paper are presented in Appendix I.

SILVICS AND SILVICULTURE OF PINE FORESTS

Jack Pine

Jack pine grows farther north than any other American pine (fig.1). It occurs in regions where rainfall is rather low and the frost-free period ranges from 80 to 120 days. The species can sustain itself on quite dry sandy or gravelly soils, but does best on well-drained loamy sands (Fowells 1965). Jack pine is most often found on areas which have been burned. This species is a major component of four forest cover types. It is dominant in the jack pine type, and shares dominance with

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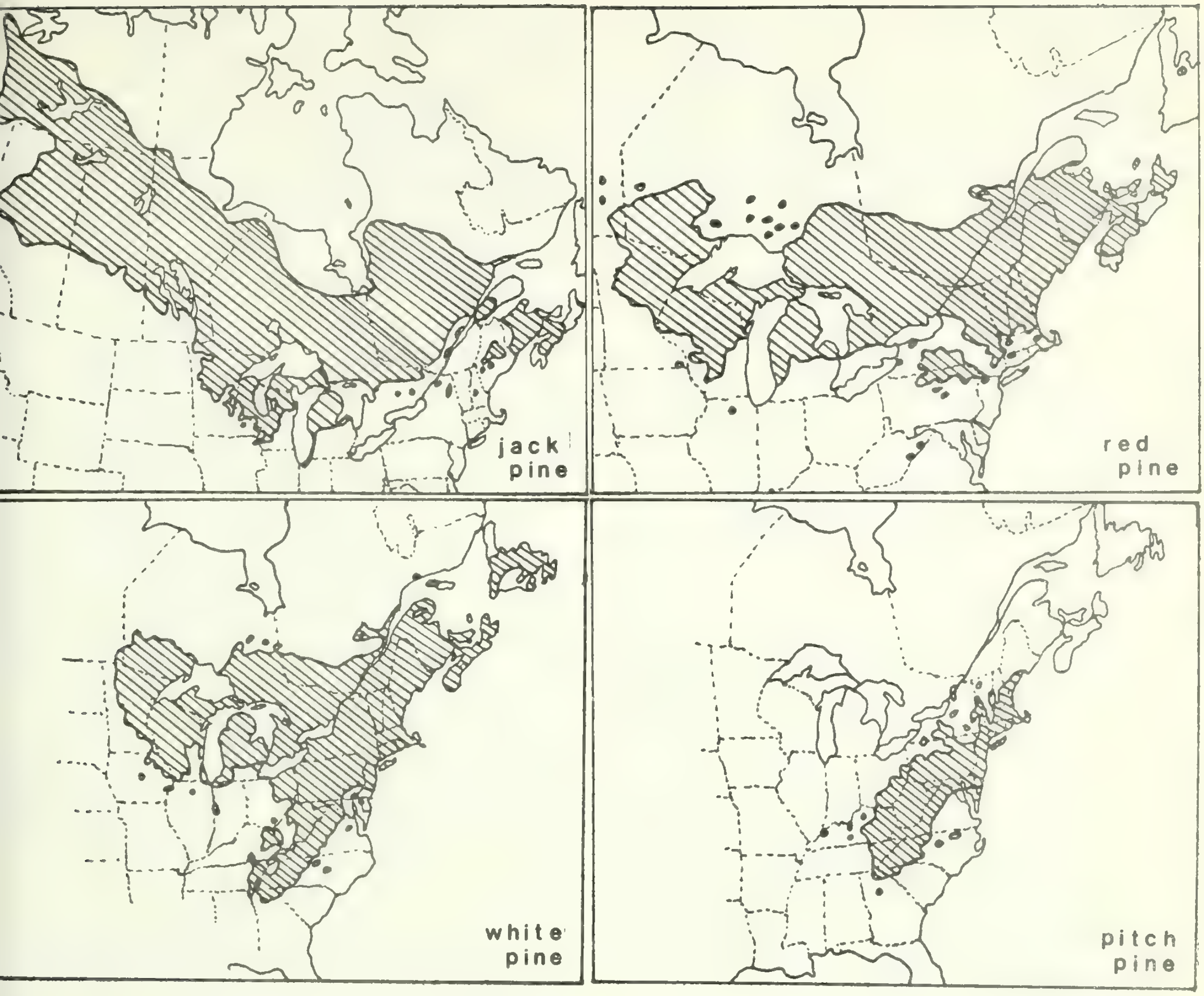

Figure 1.--Ranges of pine forests in north central and northeastern United States and Canada (Little 1971).

paper birch, black spruce, and aspen in other types.

Jack pine characteristically has serotinous cones, which usually do not open until exposed to fire or ground surface temperatures. Nonserotinous cones are common in limited portions of the range (Benzie 1973a). Regeneration is by seeding and usually follows fire. Both germination and seedling survival is best on mineral soil where there is some shade (Fowells 1965).

Jack pine is quite intolerant of shade, and usually functions as a pioneer species. It is one of the fastest-growing conifers in its range for the first 20 years. In the absence of fire, jack pine is usually replaced by more tolerant species, but may form an edaphic climax on the poorest, driest sites (Fowells 1965).

Jack pine currently occupies about 1 million hectares of forest land in the Lake States, but this acreage is decreasing as jack pine stands are converted to other species (Benzie 1977a). Overall management objectives are twofold (Benzie 1977a): (1) to maintain the jack pine type where it is the best suited species, i.e. on dry, outwash, sandy soils; and (2) to replace it with more productive species on better sites at the end of the jack pine rotation.

Clearcutting is the recommended silvicultural system for harvesting mature trees (Benzie 1973a, 1977a). The serotinous cones on slash from clear-cuts will open and seed naturally with normal ground-surface temperatures. Intensive site preparation, which usually involves prescribed burning, and planting or broadcast seeding is also used. The seed tree system is an alternative practice, but prescribed burning is necessary to prepare the seedbed and open serotinous cones. A shelterwood system is recommended as another alternative, but is most practical in well-stocked stands where cones are nonserotinous (Benzie 1973a).

Jack pine is a short-lived species, hence rotation ages are less than recommended for other pines. Stands are often cut for pulpwood at 40 to 50 years of age with no intermediate commercial thinnings. Thinnings may be prescribed on better sites where merchantable poles and sawtimber may be grown on 70-year rotations. Numerous diseases and insects affect jack pine and prompt managers to restrict rotation ages as much as possible.

Red Pine

The present range of red pine corresponds closely with areas affected by late Pleistocene glaciation (fig. 1). Its distribution corresponds with a zone of low to moderate rainfall, and frost-free periods which range from 80 to 160 days. Red pine grows on better soils than jack pine, and is found chiefly where soils are acidic and have good drainage and aeration. The species is a component of three forest cover types: red pine, jack pine, and white pine. Most species associated with red pine, except white pine, are usually found in the understory (Fowells 1965).

Reproduction is by seed and regeneration is most successful on mineral soil. Seedlings will not grow beneath heavy litter, sod, dense slash, or heavy ashes. Many old-growth stands have been established after fire when a good seed year corresponded with a light cover of ashes. Red pine seedlings grow slowly, and shaded seedlings may require 15 years to reach breast height. Growth rate is more rapid from the sapling stage to maturity, however, and basal area growth may still be constant at 200 years of age (Fowells 1965).

Red pine is less tolerant of shade than most of its associates, but more so than jack pine (Fowells 1965). A forest sere in the Lake States may be from jack pine to red pine to white pine, and finally to northern hardwoods. On infertile, sandy sites, succession may stop short of hardwoods, and red pine may be a persistant subclimax (Benzie 1973b). In the eastern portion of its range, red pine may be a successional stage in a spruce-fir or hemlock climax, rather than a climax of northern hardwoods.

A century ago, red pine covered about 2.8 million hectares of forest land in the Lake States. Today it covers only a little more than 400,000 hectares, mostly planted since 1930 (Benzie 1977b), and is the most intensivel managed coniferous type in the region. The usual management objective is to grow red pine in essentially pure, even-aged stands. Benzie (1973b) stated that clearcutting is the most commonly used silvicultural practice, and considered seed tree systems inefficient. However, Heeney (1978) recommended against clearcutting, in favor of seed tree or shelterwood systems. A strip-shelterwood practice is often employed where narrow strips of mature trees are left in an initial cut which completely clears wider strips. A later cut, after regeneration of the clearcuts, removes the mature trees and leaves the narrow strips to be used as access for later operations (Benzie 1973b, Heeney 1978).

The most favored management for red pine involves all the forestry operations which are commonly associated with pine monocultures (Benzie 1977b). Site preparation often involves mechanical treatment, herbicidal applications, and/or prescribed burning. Broadcast seeding is encouraged, but the most reliable method of establishing a red pine stand is to plant nursery-grown trees. Treatments to release seedlings usually involve herbicides. Mechanical cleaning is often needed when the trees are in the sapling stage. Thinning is advisable in the pole and sawtimber stages and stands that are thinned regularly need artificial pruning to produce good saw logs. Prescribed burning is recommended to reduce undergrowth before harvesting a mature stand. Rotations of 60 to 100 years are most commonly recommended, but the maintenance of some old growth stands to 200 years of age is suggested.

Eastern White Pine

The range of eastern white pine corresponds with a cool, humid climate and a growing season of 100 to 200 days (fig. 1). White pine grows on practically all soils within its range, but is most closely associated with well-drained sandy soils. The species is a major component of four forest types, one of which is the white pine type, and is an associate in 14 other types (Fowells 1965).

Regeneration is exclusively by seeding, and good seed crops occur at intervals of 3 to 5 years (Fowells 1965). A seedbed of moist, mineral soil is necessary for germination. Scarification and prescribed burning are often used to create favorable seedbeds (Little et al. 1973). Early growth of white pine is slow, but becomes more rapid between 10 and 20 years. It is a long-lived species and almost never ecomes stagnant in pure stands (Fowells 1965).

Ecologically, white pine is a versatile pecies and may function as a pioneer, a long- ived intermediate, or a component of the limax forest. It is considered to be inter- ediate in tolerance to shade, but is quite isceptible to shade when in the slow-growing eedling stage (Fowells 1965).

Little et al. (1973) list clearcutting, rip cutting, seed tree cutting, shelterwood itting, and group selection as the silvicul- iral methods used in regenerating white pine. me foresters believe that white pine cannot icceed itself, and indeed, this is partially rue without proper forest management practices. two-cut shelterwood system is the preferred ractice (Lancaster and Leak 1978). The first it removes 40 to 60 percent of the overstory id is made during or immediately after a good eed year. The second cut to remove the ielter trees comes 5 to 10 years later when ie seedlings have begun a rapid growth. It s often recommended that hardwood regenera- ion be treated with a herbicide before the irst cut and sometimes repeated before the econd cut (Lancaster and Leak 1978).

Many of the stand prescriptions in Lan- aster and Leak's (1978) silvicultural guide iggest management of white pine in harmony ith hardwoods where site conditions are good. roup selection is often the recommended sil- icultural practice in these stands.

Pitch Pine

Pitch pine grows in humid climates along ie Atlantic coast (fig. 1). Its distribution s spotty because it is usually found on poor, iallow soils of sandy or gravelly texture. does, however grow in a wide range of mois- ire conditions. The species is a minor com- onent in 12 forest cover types, but is only ominant in one type. It is often found in ssociation with one of several species of crub oaks (Fowells 1965).

The most extensive stands of pitch pine re found in southern New Jersey (Fowells 965). Here, the "pine barrens" occupy over 70,000 ha of wildlands which are only minutes way from Philadelphia and New York City (Mc- ormick 1970). The region is almost entirely ree from industrial and agricultural develop- ent. Pitch pine forests are of little, if ny, commercial importance for timber.

The ability of pitch pine to regenerate egetatively is outstanding. Dormant buds, ften protected in seedlings by a basal crook, prout prolifically after fire or other damage o the stem. The form and growth rates of sprouts decrease with increased age of the root crown beyond 20 years. Wildfires at frequent intervals, then, can result in a stand of slow-growing sprouts from old root systems. Pitch pine may live for 200 years, but growth starts to decline as early as 20 years of age (Fowells 1965). It is a species which is intolerant of shade, and requires mineral soil for germination. Fire has largely maintained the pitch pine type, and has been responsible for the sprout origin and poor form that characterize the species (Little and Moore 1949, Fowells 1965).

AVIAN COMMUNITIES

I have restricted the discussion of avian communities of northeastern pine forests to the breeding season. This limitation is necessary because published information pertains largely to breeding birds, and is somewhat justified because the number of terrestrial bird species may be reduced by as much as 50 percent in the winter months (calculated from Gauthreaux 1978). It should be recognized, however, that pine forests may be more important habitats for birds in the winter, than during the nesting season, because of an energetic advantage provided by dense foliage (Kelty and Lustick 1977).

Data from published breeding bird censuses (*Audubon Field-Notes* and *American Birds*) were summarized for this discussion of the composition of avian communities and trends in avian succession which correspond to the forest sere. I divided this section into communities characteristic of white, red, and jack pine forests and those of pitch pine forests. This division was rationalized because of structural, silvical, and silvicultural similarities among white, red, and jack pine forests and corresponding differences in pitch pine environments. It is widely accepted that breeding birds select habitats on the basis of vegetative structure rather than plant species composition (Hilden 1965, Balda 1975, and others).

White-Red-Jack Pine

Species Composition and Richness

The Kirtland's warbler, an endangered species, and the pine warbler, which is never abundant, are the only two species which occur in the northeastern states and are found exclusively in pine forests. Numerous species occuring predictably in pine forests, but also present in other coniferous types, deciduous types, or mixed pine and hardwood forests are the black-capped chickadee, red-breasted nuthatch, golden-crowned kinglet, ruby-crowned kinglet, yellow-rumped warbler, and chipping sparrow. Pine forests may support a rich community of breeding birds (table 1).

Table 1.--Occurrence and density of 48 species of breeding birds in seral stages of white, red, and jack pine forests. Density is expressed as number of territorial males per 10 ha: xxxx = ≥ 10; 5 ≤ xxx < 10; 1 ≤ xx < 5; x < 1. Frequency indicates the number of times each species occurred in published breeding bird censuses (*Aud. Field-Notes* and *Am. Birds*).

	Seral stages				
Breeding birds	Seedling, sapling[1]	Pole	Mature	Mixed pine/hardw.	Total freq.
Common flicker	-	-	-	xx 1	1
Pileated woodpecker	-	-	-	x 1	1
Yellow-bellied sapsucker	-	-	xx 1	xx 1	2
Hairy woodpecker	-	-	-	x 1	1
Downy woodpecker	-	-	-	x 1	1
Great-crested flycatcher	xx 1	-	xx 1	-	2
Eastern wood pewee	xx 1	-	xx 1	xx 2	4
Olive-sided flycatcher	-	-	-	x 2	2
Blue jay	x 1	xx 3	x 3	-	7
Black-capped chickadee	xx 1	xx 3	xx 2	x 2	8
White-breasted nuthatch	-	-	x 1	x 1	2
Red-breasted nuthatch	-	-	xx 2	-	2
Brown thrasher	xx 4	-	-	-	4
American robin	xx 3	xxxx 1	xx 3	xx 2	9
Hermit thrush	-	xx 2	x 2	xx 2	6
Wood thrush	-	-	xx 2	-	2
Veery	-	-	xx 3	xxx 1	4
Golden-crowned kinglet	-	-	xx 1	-	1
Ruby-crowned kinglet	-	-	x 1	-	1
Cedar waxwing	xx 3	xx 1	-	xx 1	5
Solitary vireo	-	-	x 2	x 1	3
Red-eyed vireo	x 1	-	xx 2	xx 2	5
Black & white warbler	-	xx 1	xx 2	x 2	5
Nashville warbler	xx 1	xx 2	-	-	3
Yellow warbler	x 1	xxxx 1	-	-	2
Magnolia warbler	xx 1	-	-	xx 1	2
Yellow-rumped warbler	xx 1	xx 2	xx 2	xx 1	6
Black-throated green warbler	-	-	xxx 2	xx 2	4
Blackburnian warbler	-	-	xxx 3	x 2	5
Chestnut-sided warbler	-	-	-	x 2	2
Pine warbler	-	-	xxx 1	-	1
Kirtland's warbler	x 1	-	-	-	1
Ovenbird	-	xx 3	xxx 4	x 2	9
Mourning warbler	-	xx 1	-	xx 1	2
Common yellowthroat	xx 2	xxx 1	-	xx 2	5
Canada warbler	-	-	xx 1	xx 1	2
American redstart	-	-	-	x 2	2
Scarlet tanager	-	-	xx 2	x 1	3
Rose-breasted grosbeak	x 1	-	x 1	x 1	3
Purple finch	xx 2	-	xx 1	x 1	4
American goldfinch	xxx 1	xxx 1	xx 1	x 2	5
Rufous-sided towhee	xx 2	xxx 3	xx 2	x 1	8
Vesper sparrow	xx 3	-	-	-	3
Dark-eyed junco	xxx 1	-	xx 3	x 1	5
Chipping sparrow	xxx 4	xxxx 1	xx 3	xx 1	9
Field sparrow	xxx 3	xx 1	-	-	4
White-throated sparrow	x 1	-	x 2	xxx 2	5
Song sparrow	xxxx 2	xx 1	-	xxx 1	4
Number of censuses	4	4	4	2	14

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[1] One of the young sapling study plots contained some scattered dead hardwoods, which resulted in the occurrence of species such as great-crested flycatcher and black-capped chickadee.

Table 2.--Richness and density of breeding birds in seral stages of white, red, and jack pine forests. Refer to Appendix II for additional habitat and census data.

Forest stand description	Size of study plot (ha)	No. species	No. territories		Location, Reference
			Study plot	Km^2	
Jack pine regeneration	6.5	12	12.5	193	Michigan, Munn 1974
Young red pine plantation	4.8	6	15	312	Ontario, MacDonald 1965
Young mixed pine plantation	8	31	62.5	813	Ontario, Oelke 1967a
Pole-stage white pine plantation	7.5	7	11.5	153	Massachusetts, Lloyd-Evans 1975b
Pole-stage red pine plantation	4.8	1	1	21	Ontario, MacDonald 1965
Pole/mature jack pine forest	28	11	25	88	Ontario, Erskine 1971
Mature jack pine forest	12	14	50	417	Minnesota, Niemi 1974
Mature white pine forest	7	27	50.5	694	Ontario, Oelke 1967b

Richness (i.e. number of species) is char- teristically lower in coniferous forests an in deciduous or mixed forests (Tramer 69); and pure pine forests do not provide ception to this rule (Driscoll 1977, Dickson 78, Meyers and Johnson 1978). Table 2 con- ins a summary of the findings of eight bird nsuses in seral stages of white, red, or ck pine stands. Fewer than 15 species of rds were present on all but two plots, and attered hardwoods on these two areas may have counted for the increased richness (appendix). Twenty or more species are characteristi- lly found in deciduous stands or mixed forests Tramer 1969, Meyers and Johnson 1978).

ccessional Trends

Breeding bird censuses of pine forests ere assigned to four habitat classes: seed- ing and sapling, pole stage, mature forest, nd mixed pine and hardwoods. The first three lasses are common management delineations, hile the mixed forest class represents an ad- anced seral stage in the succession towards hardwood climax.

The seedling-sapling stage was dominated y granivorous birds and some common edge pecies (table 1). Richness was predictably ow in two studies (Munn 1974, MacDonald 1965), ut unusually high on a tract studied by Oelke 1967a) where patches of hardwoods, including nags, and nest boxes contributed to high num- ers of breeding birds (table 2).

Brooks (1970, 1975, 1977, 1978) conducted breeding bird censuses in a scotch pine plantation for 8 consecutive years and provided another example of increased species richness and density when woody vegetation was associated with young pines (table 3). The high densities of birds in Brooks' studies were largely song sparrows and chipping sparrows. The numbers of American robins and purple finches gradually decreased as plant succession progressed during the 8 years of Brooks' censuses. Accordingly, breeding pairs of common yellowthroats increased steadily as woody undergrowth increased (table 3).

The diversity of breeding birds may be at its lowest in dense pole-stage pine stands because closure of the canopy leads to elimination of the understory and ground cover. Pine plantations with trees spaced at regular intervals will feature the most complete canopy closure. The resulting dearth of nesting in closed stands was most dramatically illustrated by MacDonald (1965) who found only one territorial male, a yellow-rumped warbler, on a 4.8 ha plot in a red pine plantation. Naturally-stocked stands of pole-stage pines may have closed canopies as well, but patchy openings in the canopy are more likely and will allow development of the understory.

Species richness and density were found to increase in mature stands of pine and mixed pine and hardwood forests (tables 1,2). This observation was consistent with general trends of increasing diversity and density associated with forest succession (Shugart and James 1973, Kricher 1973). Oelke (1967b) reported a particularly rich census of breeding birds, 27 species, Table 3.--Breeding birds of an upland scotch pine plantation, Allegany Co., New York from 1970 - 1977 (Brooks 1970 - 1975, 1977, 1978).

Description of habitat: Meadow planted to scotch pine in 1958; trees trimmed annually since 1962 to 2 m high and harvested regularly since 1970; grass and forb cover between trees; choke cherry and brambles increased from 1973 - 1977. Plot was 9.3 ha with diverse edges.

Year	Species	No. territories		No. territories				
		9.3 ha	km^2	Song sparrow	Chipping sparrow	American robin	Purple finch	Common yellowthroat
1970	12	106	1144	31	26	21.5	10	1
1971	18	84	902	23	14.5	13	8	+
1972	17	108	1155	31	23	13	9	+
1973	15	89	956	23	17	11	8	2
1974	18	94	1005	28	17	10	8	4
1975	14	80	854	23	19	7.5	4	6
1976	23	105	1128	28	21	5	5	8
1977	23	86	924	25	20	4	4	9
Mean	17.5	93.8	1008.5	26.5	19.7	10.6	7	3.9
Range	12-23	84-107	854-1155	23-31	14.5-26	4-21.5	4-10	+-9
C.V.				13	19	52	33	88

Other abundant species (mean no. territories): Field sparrow (7.9), Rufous-sided towhee (3.6), American woodcock (2.7), Yellow-rumped warbler (2.6).

in a white pine forest with an open canopy and a diverse hardwood understory.

Pitch Pine

Species Composition and Richness

The checklist of birds for the pine barrens of New Jersey lists the occurrence of 144 species (McCormick 1970), but many of these are water birds, rare species, and records of migratory birds which do not nest in pitch pine forests. The breeding avifauna of pitch pine forests is characterized by few species represented by numerous individuals (table 4).

Many of the birds found nesting in pitch pine forests select the characteristic understory of scrub oaks and the blueberry and huckleberry ground cover rather than the pine overstory. The rufous-sided towhee most typifies pitch pine forests, but is a shrub and ground-dwelling species. Other species which prefer understory vegetation and predictably breed in pitch pine stands are common yellowthroats, prairie warblers, and brown thrashers. Frequent fires produce abundant cavity-nesting sites for several species of woodpeckers, black-capped chickadees, and eastern bluebirds. The open habitat of pitch pine forests is preferred by bluebirds. In addition to the abundant towhee, ground-nesting species most common in pitch pine include whip-poor-wills, common nighthawks, and ovenbirds. Only pine warblers, eastern wood pewees, and blue jays are found consistently in the canopy.

Successional Trends

Because pitch pine forests are not extensively harvested and frequent fires prevent old growth, succession is typically accelerated in the early stages and truncated before maturity. Thus the avian community is characteristi of mid-successional vegetative structure. Lloy Evans (1973, 1975a, 1977) conducted censuses which allowed comparisons of richness and abundance of breeding birds in pitch pine stands at different intervals following fire (table 5). His studies indicate that understory plants and breeding birds of the low vegetative strata responded vigorously only one year after a burn

Fables (1947, 1948, 1954) censused breedin birds in the New Jersey pine barrens for 17 consecutive years (table 6). His studies began 8 years after a fire and continued until the study plot had been free from fire for 24 years This long-term study showed remarkable stabilit in the richness and density of the avifauna of a mid-successional pitch pine forest.

SILVICULTURAL MANAGEMENT OF HABITAT

An historical and comprehensive review of man's silvicultural influence on wildlife habitat was presented by Perkins (1974). A subsequent review by Schemnitz (1976) emphasized the

Table 4.--Occurrence and density of 29 species of breeding birds in successional stages of pitch pine forests following fire. Density is expressed as number of territorial males per 10 ha: xxxx = ≥ 10; 5 ≤ xxx < 10; 1 ≤ xx < 5; x < 1. Frequency indicates the number of times each species occurred in published breeding bird censuses (*Aud. Field-Notes* and *Am. Birds*).

Breeding birds	No. years following fire				Total freq.
	0-1	2-10	11-20	21+	
Mourning dove	–	x 3	x 2	x 2	7
Black-billed cuckoo	–	x 1	x 1	–	2
Yellow-billed cuckoo	–	x 1	x 1	x 2	4
Common nighthawk	–	x 2	x 2	x 1	5
Whip-poor-will	x 2	x 3	xx 3	x 2	10
Common flicker	xx 3	x 3	x 2	x 3	11
Hairy woodpecker	xx 1	xx 1	x 1	–	3
Downy woodpecker	x 1	x 2	x 3	x 2	8
Eastern kingbird	x 2	x 2	x 1	x 3	8
Eastern wood pewee	xx 3	x 2	x 3	x 2	10
Blue jay	xx 3	x 1	x 3	x 3	10
Eastern bluebird	xx 3	x 3	x 3	x 2	11
Hermit thrush	xx 3	xx 1	–	xx 1	5
American robin	xx 2	xx 1	x 2	–	5
Gray catbird	–	x 1	x 3	xx 1	5
Brown thrasher	xx 2	xx 3	x 3	x 2	10
Black-capped chickadee	x 1	x 2	–	xx 1	4
Tufted titmouse	–	–	x 1	x 2	3
House wren	xx 1	xx 3	x 3	x 2	9
Black & white warbler	–	x 2	x 2	x 2	6
Pine warbler	–	xx 2	xx 3	x 2	7
Prairie warbler	xxxx 2	xxx 3	x 1	xxxx 2	8
Ovenbird	–	x 1	x 1	x 2	4
Common yellowthroat	xxx 2	xxx 3	xx 3	xxx 3	11
American goldfinch	–	–	x 3	x 1	4
Rufous-sided towhee	xxxx 3	xxx 3	xxx 3	xxxx 3	12
Chipping sparrow	–	x 2	x 3	x 2	7
Field sparrow	xxx 1	xx 3	x 2	xx 1	7
Song sparrow	–	x 2	x 3	x 2	7
Number of censuses	3	3	3	3	12

Table 5.--Richness and density of breeding birds in stands of pitch pine-scrub oak following fire and insect damage (Lloyd-Evans 1973, 1975a, 1977). Refer to Appendix III for additional habitat and census data.

Descriptive variables	Forest stand identification					
	IV-74	IV-75	III	II	V	I
Size of census plot (ha)	7.5	7.5	7.5	7.5	7.5	7.5
Years after fire	0	1	2	10	1/	30
No. bird species	6	18	13	16	22	12
No. territories	16	33	46	60	38	52
Territories/km^2	207	440	553	807	500	693

1/ 5 years after insect infestation killed pines.

Table 6.--Breeding birds of typical New Jersey pitch pine barrens, 1938-1954 (Fables 1947, 1948, 1954).

Description of habitat: 1930- most of plot was burned; 1938- pine regeneration 2 m high, scrub oak 1.6 m high; 1941- burned and unburned areas similar in appearance; 1945- pine spreading laterally; 1954- nine summer homes erected on plot. Study plot was 31 ha and included a 2 ha cedar bog.

			No. years after 1930 fire		
			8-12 (1938-42)	13-18 (1943-48)	21-24 (1951-54)
Species	Mean (15 yrs)[1]	Range	Mean no. territories		
Rufous-sided towhee	20.7	12-33	16	22	24
Prairie warbler	7.4	3-15	8	9	4
Common yellowthroat	4.9	3-8	5	5	4
Whip-poor-will	2.8	1-7	1	4	2
Pine warbler	2.7	1-8	3	3	1
Brown thrasher	2.5	1-4	3	3	2
Gray catbird	2.5	0-5	2	3	2
House wren	2.3	0-5	3	2	1
Chipping sparrow	2.2	1-4	2	3	2
Field sparrow	1.9	0-4	3	2	1
Total no. species	35.1[2]	30-42	35	35	35
Total territories	87.3	64-104	81	94	88
Territories/km^2	277	208-338	270	275	287

[1] Data from 1949-50 not available.

[2] Many species were associated with diverse habitats adjacent to the study plot.

many investigations where effects of silvicultural practices on single species of wildlife were studied. Current and future research must concentrate on silvicultural management of entire faunal communities to complement management philosophies which are increasingly holistic in scope.

Philosophies of Management

Wildlife management, if not most resource management, has been characterized in the past by a single agency implementing decisions concerning a single resource. The philosophy still prevails on much federal, state, and private land, but was legally altered on Natinal Forests in 1960 with the passage of The Multiple Use and Sustained Yield Act. This act dictated a change in thinking and in practice, but multiple-use, nevertheless, has been implemented more by decree and compromise than by design. The trade-offs necessary for scientific multiple-use management depend upon an improved knowledge of inputs and outputs of a resource system (Ripley and Buffington 1974), and upon a better understanding of public desires (Payne and Thomas 1974).

The philosophy of simultaneous consideration of multiple resources led to the featured species concept of managing wildlife (Holbrook 1974, Zeedyk and Hazel 1974, Gould 1977). This concept represented a hybrid between single-species and multiple-resource management. It was predicated on the management of a single wildlife species, but recognized that maximization of both the wildlife resource and the timber resource must be compromised. The featured-species concept should be regarded as no more than a step in the right direction towards a more comprehensive system of management.

A current management philosophy, one with an ecological rather than an economical foundation, is a multi-species concept based on providing habitat diversity (Siderits 1975, Siderits and Radtke 1977). Natural diversity should be pursued, but maximum diversity *per se* is not a suitable management objective (Webb 1977, Weins 1978). High diversity is often equated with ecosystem stability, but that relationship is questionable and is currently being tested (Goodman 1975).

The ultimate management objective is to base decisions on the balance of entire ecosystems. Ecosystem management is a concept which is being addressed by research ecologists (Wagner 1977) as well as resource managers (Grau et al. 1976). Wagner (1977) stated that ecosystem management will ultimately depend upon an understanding of energy flow and community structure.

Principles of Managing Avian Communities

Lack (1933) was one of the first to study habitat selection by birds, and since his early studies much research has addressed resource division among avian species. Many of these studies have been conducted in the last decade or two and complement each other so well that I have identified the following "principles" of managing habitat for avian communities.

1. *Habitat structure is more important in resource partitioning than other dimensions of the ecological niche.* The ecological niche, as defined by Hutchinson (1958), consists of many dimensions, one of which may be comprised of the structural components of the habitat. This dimension is often referred to as the *habitat niche* (Smith 1977). Schoener (1974) reviewed resource partitioning and concluded that for birds habitat dimensions were more important than food-type dimensions or temporal dimensions. He also stated that as the number of species increased, the number of niche dimensions must increase as well. This consideration leads to the conclusion that the diversity of bird species will be strongly dependent upon habitat diversity. Furthermore, diverse habitat for birds may be largely equated with diverse vegetative structure (see Balda 1975 for review).

A classic study by MacArthur and MacArthur (1961) documented a strong relationship between the diversity of breeding birds in a forest and layers of foliage. The results of MacArthurs' study became so widely accepted that biologists (e.g. Meslow 1978) commonly equated vegetative structure with foliage height diversity. Vegetative structure may be defined by many variables, however, and foliage height is only one component of the habitat niche. The recent uses of multivariate statistical analyses in studies of habitat structure have identified numerous habitat variables that may be important in the management of avian habitat (James 1971, Anderson and Shugart 1974, Shugart et al. 1975, Conner and Adkisson 1976).

2. *Plant succession determines avian species composition, diversity, and biomass.* The fact that certain species of birds are characteristic of different stages of the forest sere is well accepted and has been documented in many forest types (Adams 1908, Johnston and Odum 1956, Kendeigh 1948, Martin 1960, Karr 1968). Seed-eating sparrows are predictably found in bare fields and grassland just as bark-probing woodpeckers are associated with mature forests.

Theoretical properties of succession were presented by Margalef (1968) and Odum (1969). Among other attributes, it is believed that successional trends lead to increased species diversity and biomass. Species diversity is most commonly defined by a formula (Shannon and Weaver 1963) which is comprised of two components: *richness* (number of species) and *equitability* (evenness of abundance among species). Odum (1969) predicted that both components increased with succession. Species richness in breeding birds is highly correlated with diversity (Tramer 1969), and richness is commonly accepted as an index of diversity.

Breeding bird diversity roughly corresponds to expected successional trends (Johnston and Odum 1956, Shugart and James 1973, Karr 1968). However, Shugart et al. (1975) cautioned that studies of avian succession have illustrated considerable variability in diversity, and stated that a typical trend has not yet emerged. Variability is also evident when examining trends in density and biomass through succession, but the general pattern in birds is for higher values of both variables as the forest matures (Shugart et al. 1975).

3. *Avian diversity is dependent upon* (a) *vertical habitat diversity,* (b) *horizontal habitat diversity,* (c) *patchiness of habitats,* and (d) *size of forest habitats.* Whittaker (1965) distinguished between within-habitat or "alpha" diversity and between-habitat or "beta" diversity. In the context of habitat management, those distinctions can be viewed as vertical foliage layering within a stand (alpha-diversity), and the juxtaposition of stands of different successional stages and species composition (beta-diversity). Overall avifaunal diversity can be enhanced by increasing opportunities for the vertical distribution of birds within a stand (Dickson and Noble 1978), and/or by providing structural diversity among stands (Edgerton and Thomas 1978, Wiens 1978). This is to say that total avifaunal diversity is greater in the entire forest sere than in any particular seral stage.

Spatial heterogeneity also determines avian diversity. This concept is referred to as habitat patchiness and is least likely to be achieved under intensive even-aged forest management. MacArthur et al. (1962) and Roth (1976) found high correlations between bird species diversity and indices of spatial variability.

The size of forest habitats and the fragmentation of forests should be important concerns in formulating management plans which consider habitat for nongame birds (Forman et al. 1976). Galli et al. (1976) found increased species richness as the size of forest islands increased. "Habitat islands" have also been studied by Whitcomb (1977) and MacClintock et al. (1977). Their research suggested that certain bird species of the forest interior will occur only in large blocks of habitat, although the size of these blocks may be reduced if "habitat corridors" prevent isolation. The importance of habitat islands and corridors is evident, but implications for management are poorly understood at the present time.

4. *Habitat management for nongame birds should consider species assemblages.* It is unlikely that extensive nongame bird management will be conducted on a single-species basis; and I cautioned earlier against managing solely for maximum diversity. Rather, habitat management should be oriented towards carefully-defined groups of species. Several approaches have been suggested to identify suitable species assemblages. *Guilds* contain functionally related species that show similarities in foraging, nesting, and food habits. Theoretically, birds in different guilds do not compete for resources. Assigning birds to guilds may be helpful in identifying management assemblages, but tolerances of individual species to specific niche dimensions should not be overlooked.

Thomas et al. (1976) assigned species to 16 different *life forms*. It was predicted that most species of any life form would respond similarly to a specified management practice. Webb et al. (1977) used experimentation to determine that certain groups of birds responded in predictable ways to habitat alteration. Webb (1977) identified *response groups*, such as the blackburnian warbler group that responded adversely to even a partial removal of the forest canopy. Such response groups might be identified by multivariate statistical techniques such as cluster analysis, utilized by Evans (1978).

General Effects of Even-Aged Management

Even-aged forest management is, and will probably continue to be, the overriding silvicultural practice in forests of white, red, and jack pine. Previous authors (Edgerton and Thomas 1978, Meslow 1978) have predicted the following general effects of even-aged management on bird habitat.

(1) *Early stages of succession are accelerated* through practices of intensive site preparation, seeding, and planting. These practices lead to the rapid replacement of early successional bird species by those that select shrub and sapling habitat.

(2) *Old growth habitats are commonly eliminated.* Long rotations are uncommon in managed pine forests hence the diverse avian communities of mature stands are not encouraged.

(3) *Snags and cavities are often eliminated* by thinning or are not allowed to develop because of short rotations. This effect is more characteristic of intensive clearcutting than of other even-aged practices.

(4) *Monocultures are encouraged.* Monocultures usually lack diverse vegetative structure. They are susceptible to damage from diseases and insects which may lead to preventative measures such as chemical treatments and shortened rotations. For birds, the cures may be worse than the diseases.

Silvicultural Recommendations

Regeneration Cutting

Commercially important northern pine forests managed in even-aged stands are harvested by clearcutting, shelterwood, or seed tree cutting. Clearcutting has the most obvious impact on the vertical structure of habitat and will result in a conversion of the avian community. Such conversions will *generally* reduce species richness and biomass. This may not be the case in pine stands, however, because they are often harvested when commercially mature, rather than ecologically mature, hence richness and biomass may already have been at a minimum.

Clearcutting followed by intensive site preparation effectively reduces the habitat niche to only two dimensions and strongly impacts bird populations. The effects are usually of short duration, however, because herbaceous cover develops rapidly on the burned areas. Clearcutting with *natural regeneration* is a preferred alternative.

The other even-aged management alternatives shelterwood and seed tree harvesting are much less disruptive to the avian community. Although much of the habitat structure is removed by both methods of harvest, opportunities for several functional groups of birds are preserved through the seed-producing trees which are left.

If clearcutting is the selected management option, the size, shape, and location of clearcuts can be planned to enhance avian communities Wildlife biologists have long maintained that clearcut areas should be intermixed as much as possible to produce a habitat with maximum horizontal diversity. However, we have never agreed on an optimum size for these clearcuts. The smaller the cuts, and the greater the admixture of age-classes, the more edge is provided; and wildlifers traditionally have been taught to manage for the edge.

Edge habitat might not be in short supply in a harvesting scheme involving clearcuts of different ages; but areas in the forest interior might be, and there are "forest-interior species" just like there are edge species. How large should stands be to provide for the species of forest interiors? Research on this subject is needed (see Robbins, this Proceedings). This may be merely an academic question in intensively managed pine forests, because forest interior species are usually associated with old-growth habitat. Hence, managers must first lengthen the rotation period to produce mature stands, then be concerned for species of the forest interior.

Intermediate Treatments

Intensive pine silviculture and habitat enhancement for birds are often in conflict as stands develop. The removal of hardwood regeneration by chemical or mechanical means drastically reduces the vertical structure of developing pine stands. On a short-rotational system, maximum avian diversity may occur in the sapling stage prior to closure of the overstory, but pre-commercial thinning to remove the hardwood understory will prevent a rich avifaunal composition in the sapling stage.

After crown closure, pine stands often reach a successional low-point in avian diversity. Thinning can improve the habitat at this point. If at all feasible, thinning or other timber stand improvement should be done in a random pattern to create patchiness in the stand. Standard row-thinning provides ephemeral stimulation of the understory at best. Stem girdling is a stand improvement practice which may be particularly beneficial to birds.

Pine Forest Types

Jack pine should be maintained on poor sites where it will not be out-competed. Habitat for birds will likely be improved by periodic fires. Conversion of jack pine to a more productive forest type is recommended on better sites. Red pine is often selected to replace jack pine, and it is with red pine that the silvicultural recommendations presented above are most applicable.

Many silvicultural options are available in forests of white pine. Shelterwood and seed tree systems or clearcutting in strips or patches are practices which may provide productive wildlife habitat. White pine may also be managed in uneven-aged stands. On good sites, group selection for white pine in association with management for hardwoods will provide excellent habitat for birds.

Management of pitch pine forests should highlight preservation and the encouragement of occasional fires. Conversion to a non-forested condition is the greatest threat to this forest type, although much pitch pine acreage is currently preserved as state-owned forest land.

KIRTLAND'S WARBLER--AN ENDANGERED SPECIES

The Kirtland's warbler has always been a rare species. Not until 1903 were the nesting grounds found in northern Lower Michigan. Singing males, censused as an index to the nesting population, have declined from 500 in 1961 to 200 in 1971 and have remained at or below that number (Byelich et al. 1976).

The breeding habitat requirements of the Kirtland's warbler are highly specialized (Radtke and Byelich 1963, Byelich et al. 1976). They nest in young stands of jack pine 80 ha or more in size, where homogeneous groups of pine occur in patchy distributions, interspersed with areas of small, grassy openings. The species nests on the ground usually under living pine branches near the ground. Suitable habitat is present only when jack pines are between 2 m and 5 m in height which normally occurs when the trees are 8 to 21 years of age. Preferred nesting habitat is found almost exclusively on a single soil type, Grayling sand.

Byelich et al. (1976) identified two factors which were limiting the population of Kirtland's warblers on the breeding grounds. The primary factor was a reduction in suitable nesting habitat because of fire control and other recent forest practices (Mayfield 1963). A second limiting factor was egg parasitism of Kirtland's warbler nests by brown-headed cowbirds. (Mayfield 1977).

Habitat management for the Kirtland's warbler is the epitome of single-species management, but is dictated by society's concern for a species faced with extinction and, of course, the Endangered Species Act of 1973. Preservation of this species is being carried out in accordance with a recovery plan approved by the U.S. Fish and Wildlife Service (Byelich et al. 1976).

Management of nesting habitat is designed to allow the reestablishment of a self-sustaining population of 1000 pairs of Kirtland's warblers throughout the known former range. The Michigan Department of Natural Resources is currently managing over 30,000 ha of state-owned land for the species, and the Huron National Forest has designated 55,400 ha as Kirtland's warbler habitat (personal communication, Michael T. Mang, William Irvine). These lands are being managed in blocks of 80 to 120 ha, where even-aged stands of jack pine are being regenerated at 10-year intervals. Clearcutting, burning, planting, and seed tree cutting are being used to create the desired habitat. Approximately 25 percent of each block is left in small openings. The management agencies opted to utilize the jack pine for commercial pulpwood thus doubling the total acreage of management blocks and harvesting on a 45 to 50-year rotation.

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Appendix I .--Nomenclature of birds and plants mentioned in the text.

Birds

American woodcock	*Philohela minor*
Mourning dove	*Zenaida macroura*
Yellow-billed cuckoo	*Coccyzus americanus*
Black-billed cuckoo	*Coccyzus erythropthalmus*
Whip-poor-will	*Caprimulgus vociferus*
Common nighthawk	*Chordeiles minor*
Common flicker	*Colaptes auratus*
Pileated woodpecker	*Drycopus pileatus*
Yellow-bellied sapsucker	*Sphyrapicus varius*
Hairy woodpecker	*Picoides villosus*
Downy woodpecker	*Picoides pubescens*
Eastern kingbird	*Tyrannus tyrannus*
G.-crested flycatcher	*Myiarchus cinerascens*
Eastern wood pewee	*Contopus virens*
Olive-sided flycatcher	*Nuttalornis borealis*
Blue jay	*Cyanocitta cristata*
Black-capped chickadee	*Parus atricapillus*
Tufted titmouse	*Parus bicolor*
White-breasted nuthatch	*Sitta carolinensis*
Red-breasted nuthatch	*Sitta canadensis*
House wren	*Troglodytes aedon*
Gray catbird	*Dumetella carolinensis*
Brown thrasher	*Toxostoma rufum*
American robin	*Turdus migratorius*
Wood thrush	*Hylocichla mustalina*
Hermit thrush	*Catharus guttata*
Veery	*Catharus fuscescens*
Eastern bluebird	*Sialia sialia*
Golden-crowned kinglet	*Regulus satrapa*
Ruby-crowned kinglet	*Regulus calendula*
Cedar waxwing	*Bombycilla cedrorum*
Solitary vireo	*Vireo solitarius*
Red-eyed vireo	*Vireo olivaceus*
Black & white warbler	*Mniotilta varia*
Nashville warbler	*Vermivora ruficapilla*
Yellow warbler	*Dendroica petechia*
Magnolia warbler	*Dendroica magnolia*
Yellow-rumped warbler	*Dendroica coronata*
Black-throated green warbler	*Dendroica virens*
Blackburnian warbler	*Dendroica fusca*
Chestnut-sided warbler	*Dendroica pensylvanica*
Pine warbler	*Dendroica pinus*
Kirtland's warblar	*Dendroica kirtlandii*
Prairie warbler	*Dendroica discolor*
Ovenbird	*Seiurus aurocapillus*
Mourning warbler	*Oporornis philadelphia*
Common yellowthroat	*Geothlypis trichas*
Canada warbler	*Wilsonia canadensis*
American redstart	*Setophaga ruticilla*
Scarlet tanager	*Piranga olivacea*
Rose-breasted grosbeak	*Pheucticus ludovicianus*
Purple finch	*Carpidacus purpureus*
American goldfinch	*Carduelis tristis*
Rufus-sided towhee	*Pipilo erythrophthalmus*
Vesper sparrow	*Pooecetes gramineus*
Dark-eyed junco	*Junco hyemalis*
Chipping sparrow	*Spizella passerina*
Field sparrow	*Spizella pusilla*
White-throated sparrow	*Zonotrichia albicollis*
Song sparrow	*Melospiza melodia*

Plants

Eastern white pine	*Pinus strobus*
Red pine	*Pinus resinosa*
Jack pine	*Pinus banksiana*
Pitch pine	*Pinus rigida*
Scotch pine	*Pinus sylvestris*
Balsam fir	*Abies balsamea*
Black spruce	*Picea mariana*
Eastern hemlock	*Tsuga canadensis*
Paper birch	*Betula papyrifera*
Quaking aspen	*Populus tremuloides*
Choke cherry	*Prunus virginiana*
Scrub oaks	*Quercus ilicifolia*
- - -	*Quercus prinoides*
- - -	*Quercus minor*
Blueberry	*Vaccinium angustifolium*
- - -	*Vaccinium vacillans*
Huckleberry	*Gaylussacia baccata*
Wintergreen	*Gaultheria procumbens*
Bracken fern	*Pteridium aquilinum*

Appendix II.-Breeding birds in seral stages of white, red, and jack pine forests.

Descriptive variables	Young jack pine regeneration	Young red pine plantation	Young mixed pine plantation	Pole stage white pine plantation
Year of census	1974	1962	1967	1974
Size of plot (ha)	6.5	4.8	8	7.5
Location	Michigan	Ontario	Ontario	Massachusetts
Habitat				
Stand history	Fire in 1964	Planted in 1950	Reforested agricultural area	Planted in 1933-35
Overstory	Numerous dead snags	None	Scattered hardwoods	White pine dominant (61% cover)
Understory	Young jack pine	Young red pine	Jack, red, scotch, white pines	Scrub oak (5% cover)
Ground cover	Dense	Dense	Dense	Sparse
Edge	Uniform habitat	N/A	Fairly uniform	Uniform habitat
Breeding Birds				
No. species	12	6	31	7
No. territories	12.5	15	62.5	11.5
Territories/km^2	193	312	813	153
Species and no. territories/plot[1/]	Brown thrasher 2.5	Dark-eyed junco 4	Field sparrow 8.5	Ovenbird 4
	Vesper sparrow 2	Vesper sparrow 4	Chipping sparrow 5	Rufous-sided towhee 2.5
	Chipping sparrow 2	Chipping sparrow 3	Song sparrow 3.5	Black-capped chickadee 2
	Field sparrow 2	American robin 2	Cedar waxwing 2.5	Blue jay 1
	E. bluebird 1.5	Brown thrasher 1	Purple finch 2	Hermit thrush 1
Reference	Munn 1974	MacDonald 1965	Oelke 1967	Lloyd-Evans 1975b

Appendix II.-Continued.

Descriptive variables	Pole stage red pine plantation	Pole/Mature jack pine forest	Mature jack pine forest	Mature white pine forest
Year of census	1962	1971	1974	1967
Size of plot (ha)	4.8	28	12	7
Location	Ontario	Ontario	Minnesota	Ontario
Habitat				
Stand history	N/A	N/A	N/A	N/A
Overstory	Red pine - closed	Jack pine, open and closed	Jack pine dominant (59% cover)	White pine canopy (40-50% cover); diverse subcanopy
Understory	Sparse	Sparse	Moderate	Sparse (5-10% cover)
Ground cover	Sparse	Moderate	Dense (78% cover)	Sparse (5% cover)
Edge	N/A	Uniform habitat	Uniform habitat	Moderate diversity
Breeding Birds				
No. species	1	11	14	27
No. territories	1	25	50	50.5
Territories/km^2	21	88	417	694
Species and no. territories/plot	Yellow-rumped warbler 1	Hermit thrush 4.5 Ovenbird 4 Dark-eyed junco 3.5 Chipping sparrow 3 Yellow-rumped warbler 2.5	Ovenbird 12 Blackburnian warbler 10 Nashville warbler 7 Golden-crowned kinglet 4 Chipping sparrow 3	Blackburnian warbler 4.5 Pine warbler 4 Ovenbird 4 E. wood pewee 3 Wood thrush 3
Reference	MacDonald 1965	Erskine 1971	Niemi 1974	Oelke 1967

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[1] Five most abundant species are listed.

Appendix III.-Breeding birds in seral stages of pitch pine-scrub oak forest. Plots of 7.5 ha were located in uniform habitat, Plymouth Co., Massachusetts (Lloyd-Evans 1973, 1975a, 1977).

Descriptive variables	Stand IV-74 Recent burn		Stand IV-75 Recent burn		Stand III Recent burn	
Year of census	1974		1975		1973	
Habitat:						
Stand history	Burned in May 1974		Burned in May 1974		Burned in May 1971	
Dominant tree (%)	Pitch pine (90)		Pitch pine (72)		Pitch pine (100)	
Dominant understory (%)	Scrub oak (97)		Scrub oak (94)		Scrub oak	
Tree cover (%)	5		5		6	
Dominant ground cover (%)	Oak, seedlings, fern, huckleberry		Huckleberry, wintergreen, blueberry		Huckleberry, blueberry	
Breeding Birds:						
No. species	6		18		13	
No. territories	15.5		33		45.5	
Territories/km^2	207		440		553	
Species and no. territories1/	Rufous-sided towhee	6.5	Prairie warbler	10.5	Prairie warbler	9.5
	Hermit thrush	3	Rufous-sided towhee	7.5	Rufous-sided towhee	9
	E. wood pewee	2	Common yellowthroat	2	Common yellowthroat	9
	E. bluebird	2	Brown thrasher	1.5	Field sparrow	5
	Common flicker	1	E. bluebird	1.5	Purple finch	2
	Blue jay	1	House wren	1.5	Brown thrasher	1

Descriptive variables	Stand II Regenerating		Stand V Insect damage		Stand I Mature	
Year of census	1973		1976		1973	
Habitat:						
Stand history	Burned in May 1963		97% of pines killed in 1971		Burned in 1943 or 1944	
Dominant tree (%)	Pitch pine (100)		Pitch pine (100)		Pitch pine (100)	
Dominant understory (%)	Scrub oak		Scrub oak (100)		Scrub oak	
Tree cover (%)	26		4.8		70	
Dominant ground cover (%)	Blueberry, huckleberry		Huckleberry, blueberry		Huckleberry, blueberry	
Breeding Birds:						
No. species	16		22		12	
No. territories	60.5		37.5		52	
Territories/km^2	807		500		693	
Species and no. territories	Prairie warbler	19	Rufous-sided towhee	18	Prairie warbler	16.5
	Rufous-sided towhee	13	Prairie warbler	10.5	Rufous-sided towhee	13
	Common yellowthroat	9	Common yellowthroat	5	Common yellowthroat	11.5
	Field sparrow	3.5	Field sparrow	1.5	Black-capped chickadee	3
	Brown thrasher	3	Hermit thrush	1.5	Field sparrow	2
	Hermit thrush	2	Catbird	0.5	Common flicker	1

1/ Six most abundant species are listed.

EFFECTS OF SILVICULTURAL PRACTICES ON BIRD COMMUNITIES IN UPLAND SPRUCE-FIR STANDS

Hewlette S. Crawford and Richard W. Titterington[1]

Abstract.--Composition and density of bird populations in upland spruce-fir stands are influenced by the admixture of hardwood with softwoods, the vertical and horizontal structure of the stand, and the extent of spruce budworm infestation of the stand. Silvicultural practices modify all three factors and influence bird populations.

INTRODUCTION

Upland spruce-fir forest types in northeastern and north-central United States and Maritime and southern Canada are largely commercial forests, supporting major wood-using industries. In the United States, most of this forest land is privately owned; in Canada, there is more public ownership. However, in both cases, forest cutting is a major factor that modifies bird habitat structure and influences bird populations.

These commercial woodlands provide the economic base for several states and provinces. Yet the management of these forests is not intensive compared to that in other parts of the continent. Woodland owners and harvesters had enough wood to cut to meet yesterday's needs. However, the situation is beginning to change.

The demand for wood products continues to increase. In the past, industry had the western old-growth forests and the "wood basket" of the South to absorb this demand. Substantial inroads have been made on the old growth and the wood basket is not as deep or productive as once thought. These factors plus competition among the major wood-producing companies will bring intensive forestry to the northern and northeastern coniferous forests, and these practices will have a measurable impact on bird populations.

This paper discusses the effects of silvicultural practices on nongame birds in upland spruce-fir forests.

The major tree species of the upland spruce-fir type are balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and red spruce (*P. rubens*). Red spruce is limited to eastern portions of the continent, but whit spruce is found westward across the continent and balsam fir beyond midcontinent. The transcontinental belt of spruce and fir averages about 300 miles wide (Westveld 1953). Red spruce and balsam fir also grow southward in the higher elevations of the Appalachian Mountains. In West Virginia, balsam fir possibly intergrades with Fraser fir (*A. fraseri*) (Strausbaugh and Core 1964).

Spruce and fir along the northern border of their transcontinental belt are often found in almost pure stands. Intolerant hardwoods such as the birches (*Betula* spp.) and aspens (*Populus* spp.) increase toward the central latitudinal portion of this belt. Along the southern border, midtolerant and tolerant hardwoods such as beech (*Fagus grandifolia*) and maples (*Acer* spp.) compete with spruce and fir for favorable sites.

Although hardwoods are naturally more abundant in the southern portion of the upland spruce-fir type, site characteristics substantially influence their distribution and abundance. Spruce and fir on thin, infertile soils in the moist eastern portion of the range generally grow in dense stands with closed canopies and little hardwood admixture. In an undisturbed state these stands e single-storied with sparse undergrowth. re fertile soils permit more hardwood owth and increased canopy layering. In the re continental climate to the west, hard-ods are better competitors for limited soil isture, and moisture stress increases the xture of hardwoods in spruce-fir stands estveld 1953).

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BREEDING BIRD COMMUNITIES

The composition and density of bird com-nities throughout the upland spruce-fir rest are affected by three habitat features: e degree of hardwood admixture with soft-ods, the vertical and horizontal stand ructure, and the degree of spruce budworm *horistoneura fumiferana* Clem.) infestation the stands. These features can vary con-derably from forest stand to forest stand. also recognize there can be fluctuations density of bird populations from year to ar caused by factors such as winter mor-lity, migration losses, etc.

The first two features depend on such ctors as geographic location, microclimate, te characteristics, and forest management. ruce budworm infestations appear to be cy-ic in nature and are affected by weather and e amount, age, and distribution of balsam r in the stand.

To describe the relationship between bird pulations and forest habitats we analyzed nsus data from 16 forest stands representing fferent conditions in upland conifers able 1). Cluster analysis was used to ex-ess the degree of association or similarity tween the bird populations of the 16 stands. placed each of the 16 bird censuses into e of six groups based on the similarity of eir bird species composition (Fig. 1, Table):

Balsam fir stands (censuses 1 and 2)
Mature spruce stands (censuses 5,6,7,8, and 9)
Mixed growth stands (censuses 14,15, and 16)
Spruce-fir stands with budworm (censuses 3 and 4)
Spruce-fir stands without budworm (censuses 12 and 13)
Young spruce stands (censuses 10 and 11)

Balsam Fir Stands

In the two balsam fir stands, this spec-es dominated the overstory trees. The stand ocated near Lake Winnipegosis, Manitoba Erskine 1972), was characterized by a two-ier overstory with a dominant canopy (about 7 m tall) of fir and paper birch and a sub-anopy (about 9.5 m tall) of fir, birch, and uaking aspen (*P. tremuloides*). The stand ocated in west-central Saskatchewan (Erskine 1973) was characterized by dense, immature growth of balsam fir (9 to 12 m tall) and small numbers of mature fir, spruce, aspen, and birch scattered throughout (up to 25 m tall).

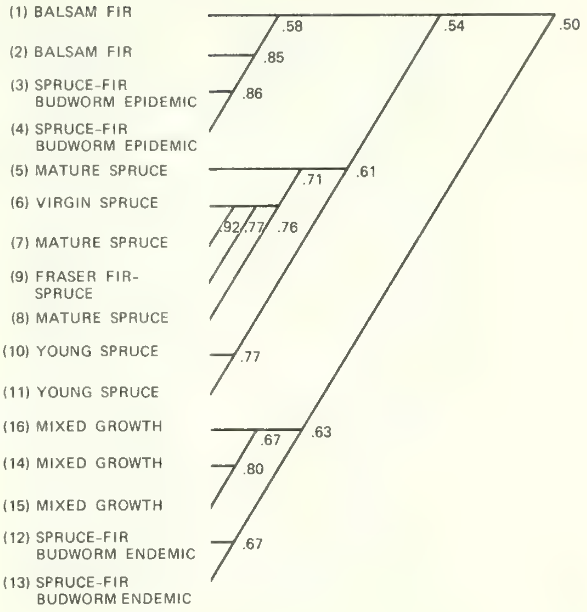

Figure 1.--Cluster diagram of forest plots based on bird species composition. Similarity indices are shown at connecting points.

The balsam fir stands supported an impoverished avifauna with an average of only 128 pairs/40 ha and 20 bird species. The four dominant bird species were the Swainson's thrush (*Catharus ustulata*) and magnolia (*Dendroica magnolia*), black-throated green (*D. virens*), and bay-breasted (*D. castanea*) warblers. The Swainson's thrush and magnolia warbler were associated with the immature balsam fir.

Qualitatively, the two balsam fir stands were similar in bird species composition to the budworm infested spruce-fir stands (Table 2). The presence of Tennessee (*Vermivora peregrina*) and bay-breasted warblers, species closely associated with spruce budworm, was probably a result of spruce budworm populations.

Table 1.--Summary of bird censuses used in analyses of bird communities in upland conifers

Census no.	Forest type	Location	No. of species	Pr/ 40 ha	Source
1	Balsam fir forest	Manitoba	20	112	Erskine (1972)
2	Balsam fir forest	Saskatchewan	19	145	Erskine (1973)
3	Spruce-fir forest budworm epidemic	Ontario	36	319	Kendeigh (1947)
4	Spruce-fir forest budworm epidemic	Maine	31	350	Stewart and Aldrich (1952)
5	Mature 2nd-growth spruce	New Hampshire	21	235	Titterington (Unpubl. data)
6	Virgin spruce forest	West Virginia	28	325	Stewart and Aldrich (1949)
7	Mature 2nd-growth spruce	West Virginia	23	295	Stewart and Aldrich (1949)
8	Mature red spruce forest	Vermont	20	217	Nichols (1968)
9	Mature Fraser fir-spruce	West Virginia	23	247	Hutton et al. (1968)
10	Young spruce	West Virginia	19	278	Stewart and Aldrich (1949)
11	Young spruce	West Virginia	15	220	Sigel et al. (1968)
12	Spruce-fir forest budworm endemic	Ontario	24	249	Martin (1960)
13	Spruce-fir forest budworm endemic	Ontario	28	131	Sanders (1970)
14	Spruce-fir-aspen-birch, mixed growth	Ontario	22	159	Martin (1960)
15	Spruce-fir-hardwood, mixed growth	Ontario	27	258	Martin (1960)
16	Balsam fir-birch forest, mixed growth	Minnesota	23	276	Niemi (1972)

Mature Spruce-Fir with Epidemic Spruce Budworm Populations

Dominant spruce and fir with overmature and dying trees, a midstory of balsam fir, and an open shrub understory botanically characterized these stands (Kendeigh 1947, Stewart and Aldrich 1952). The characteristic biological features were an ongoing spruce budworm infestation and high densities of breeding birds (Morris et al. 1958). The budworm areas supported 1.75 times as many pairs/40 ha as similar stands with endemic budworm populations (334 pairs/40 ha compared to 190/40 ha). Three warbler species, the Tennessee, Cape May (*D. tigrina*) and bay-breasted, were abundant in the budworm areas but absent from non-budworm areas (Table 2). These three species show strong positive numerical responses to spruce budworm outbreaks (Morris et al. 1958).

Spruce-Fir with Endemic Spruce Budworm Populations

Balsam fir predominated in these stands and white and black (*P. mariana*) spruce also were significant in the overstory. The overstory had a clumped distribution with several shrub species occupying the openings. Sanders (1970) found intolerant hardwoods in the overstory but Martin (1960) did not. Average heights of overstory trees were about 10 and 15 m in Sanders' and Martin's areas, respectively.

The magnolia warbler was the dominant species; yellow-rumped warblers (*D. coronata*) and golden-crowned kinglets (*Regulus satrapa*) were abundant in the overstory canopy. White-throated sparrows (*Zonotrichia albicolis*) and chestnut-sided warblers (*D. pensylvanica*), both common species, were found in the shrubby openings.

Table 2.--Density of bird populations, by species and forest type (in pairs per 40 ha: o = absent; + = <5; * = 5 to 10; ** = 11 to 25; *** = >25)

Species	Balsam fir	Mature spruce	Mixed growth	Budworm spruce-fir	Non-budworm spruce-fir	Young spruce 15-30 ft tall
Yellow-bellied sapsucker	o	o	*	+	+	o
Black-capped chickadee	o	+	*	+	+	*
Boreal chickadee	+	+	o	*	+	+
Red-breasted nuthatch	+	*	+	*	+	*
Brown creeper	o	+	o	+	o	o
Winter wren	*	+	+	+	+	**
American robin	o	+	+	+	+	**
Wood thrush	o	+	+	o	o	o
Hermit thrush	o	*	+	+	+	+
Swainson's thrush	**	*	+	**	+	**
Veery	o	+	*	+	o	+
Golden-crowned kinglet	o	***	+	*	**	*
Solitary vireo	+	**	o	*	o	o
Red-eyed vireo	+	+	***	*	+	o
Black-and-white warbler	o	o	**	o	*	o
Tennessee warbler	*	o	o	***	o	o
Nashville warbler	o	o	**	*	*	o
Magnolia warbler	**	***	**	***	***	***
Black-throated blue warbler	o	**	+	+	o	o
Cape May warbler	o	o	o	***	o	o
Yellow-rumped warbler	*	*	+	**	**	o
Black-throated green warbler	**	**	*	+	o	+
Blackburnian warbler	+	***	**	**	+	+
Chestnut-sided warbler	o	o	*	o	**	+
Bay-breasted warbler	**	o	o	***	o	o
Ovenbird	+	+	***	*	*	o
Canada warbler	*	*	**	+	o	o
Purple finch	o	*	+	+	+	*
Dark-eyed junco	o	***	o	*	+	***
White-throated sparrow	*	*	*	**	***	o
$\bar{X}$ pairs/40 ha	128	264	231	334	190	249
$\bar{X}$ species	20	23	24	34	26	17

Mature Spruce

The mature spruce stands were second growth except for one virgin stand with a considerable tolerant hardwood component. The virgin stand (Stewart and Aldrich 1949) was essentially one-storied with a sparse scattering of understory trees and shrubs. Second-growth stands were mature and contained large trees, dense closed canopies, and scattered openings with shrubs and saplings. The canopy of one stand (Hutton et al. 1968) was nearly 50 percent Fraser fir and 35 percent red spruce. Canopies in the other stands were 60 to 90 percent red spruce (Stewart and Aldrich 1949, Nichols 1968, Titterington unpubl. data). The Fraser fir stand grouped with mature spruce because the fir were unusually large trees--up to 48 cm dbh. Few balsam fir reach this size and tree size seems to be a determinant in bird populations.

These stands supported almost as many birds as the budworm-infested stands. The most abundant birds were the canopy gleaners--blackburnian warbler (*D. fusca*) and golden-crowned kinglet in the upper canopy; solitary vireo (*Vireo solitarius*), magnolia, black-throated blue (*D. caerulescens*) and black-throated green warblers in the mid- to lower canopy; and dark-eyed junco (*Junco hyemalis*) on the open forest floor. The mature spruce stands supported more than twice as many birds as the balsam fir stands, an average of 264 pairs/40 ha compared to 128 for balsam fir. Several factors may account for this substantial difference. Spruce are long lived, commonly grow taller (USDA 1965), and develop greater canopy depth than balsam fir. Spruce express dominance and provide more heterogeneous horizontal and vertical stand structure than is found in fir stands. We believe spruce stands with more foliage and limb area than fir stands support greater populations of endemic insects that are valuable as food for foliage-gleaning birds.

These bird species have adapted to divide the feeding zones and more efficiently use the mature crowns (MacArthur 1958).

Young Spruce Stands

A dense, uniform canopy of > 90 percent red spruce dominated the habitat structure of the young spruce stands. Tree heights averaged 4.5 m in one stand (Stewart and Aldrich 1949) that had a dense understory of mountain laurel (*Kalmia latifolia*), and 9 m in the other stand (Sigel et al. 1968) that was quite open underneath.

These stands supported an average of 249 pairs/40 ha of breeding birds though the young stands averaged only 17 bird species compared with an average of 23 in the mature stands. The dominant bird species were the magnolia warbler and the dark-eyed junco; both species were also common in mature spruce stands (Table 2), but their densities were twice as high in the young stands as in the mature. While the magnolia warbler is a characteristic species of the upland conifer forest, it is most populous in dense, young developing conifer stands. Dark-eyed juncos nest and forage on the ground as well as in coniferous shrubs and saplings. Both species benefit from the protective cover common in these stands.

Although sparse in mature stands, the Swainson's thrush, winter wren (*Troglodytes troglodytes*), and American robin (*Turdus migratorius*) were common in young spruce stands. The two thrushes were probably attracted to the dense saplings and pole-size softwoods. The winter wren's response to habitat features is similar to that of the dark-eyed junco.

Virtually absent from the young spruce stands were high canopy, foliage-gleaning bird species such as the golden-crowned kinglet and blackburnian and black-throated green warblers.

Mixed Growth Stands

Two of the stands (Martin 1960, Niemi 1972) contained intolerant hardwoods from 12 to 18 m tall, overtopping fir. One stand (Martin 1960) had tolerant hardwoods from 18 to 24 m tall, overtopping fir. Heights of fir ranged from 9 to 12 m. The understory in all stands consisted of a dense growth of shrubs and tree seedlings and saplings.

Red-eyed vireos (*V. olivaceous*) and ovenbirds (*Seiurus aurocapillus*) were the dominant species. Birds usually associated with hardwoods and common in these mixed growth stands were black-and-white (*Mniotilta varia*), Nashville (*V. ruficapillus*), and Canada (*Wilsonia canadensis*) warblers. Yellow-bellied sapsuckers (*Sphyrapicus varius*) were more common in this forest type than in any other. Other common species attracted to the softwoods were the magnolia and blackburnian warblers. Other species that frequent high canopy conifers were sparse or absent.

These stands supported an average of 231 pairs/40 ha, slightly less than were supported by mature spruce stands. Numbers of species were about the same as in mature spruce stands (Table 2).

SILVICULTURE AND BIRD HABITAT

Spruce and fir are tolerant and can be successfully managed with even-age or uneven-age silviculture. Seed-tree systems are not suitable because shallow rooting makes these tree species susceptible to windthrow.

Silvicultural practices modify forest stands by changing plant species composition and the vertical and horizontal structure of vegetation in the stand. Plant composition and structure are the base elements of bird habitat. Many studies have shown that bird populations respond to changes in their habitat (Hagar 1960, Haapanen 1965, Titterington et al. 1979).

We can scale stand modification from "light" (uneven-age silviculture) to "heavy" (clearcutting, followed by site preparation and planting). Between these limits lie many different silvicultural practices. Effects on bird populations differ along this approximate continuum according to the degree of habitat modification (Table 3).

Also, after any disturbance--including that caused by cutting--the patterns and timing of secondary plant succession vary with the geographic location, availability of seed, microclimate, site, and the degree of disturbance.

The successional patterns of bird species in upland coniferous forests are closely related to the plant succession that follows habitat disturbances (Titterington et al. 1979). Each seral stage is characterized by a group of associated bird species.

The following discussion is based primarily on data collected in commercially clearcut spruce-fir forests of northern Maine (Titterington et al. 1979), and on our findings in Maine upland spruce-fir stands. The response by habitat-related groups of bird species to different habitat features should be similar throughout the upland spruce-fir type. Species

Table 3.--The response of birds to habitat modification, by bird habitat group, response time, and silvicultural treatment (A = abundant in species and density; C = common; R = regular; 0 = occasional)

Response time (years)	Treatment							
	Uneven-age	Large diam-limit	Thinning sawlogs	Thinning poles	Shelter-wood cut	Commercial clearcut & small diam. limit	Silvi-cultural clearcut	Cut, site preparation, & plant
UPPER CANOPY GROUP								
0 to 5±	A	R	R	R	C	R-0	0	0
5 to 30±	A	R	C	C	0	R-0	0	0
30 to 100±	A	C	--	A-C	C-R	R-0	C	C
LOWER CANOPY GROUP								
0 to 5±	A	R	R	C	C	R-0	0	0
5 to 30±	A	R	C	C	0	R-0	R	R
30 to 100±	A	C	--	A-C	C-R	R-0	C	C
SHRUB-SAPLING GROUP								
0 to 5±	R	0	0	R	0	R-0	R-0	0
5 to 30±	R	0	R-0	R-0	C	A-C	A-C	C-R
30 to 100±	R	0	--	0	R	R-0	0	0
BRAMBLE-HERBACEOUS GROUP								
0 to 5±	0	0	0	0	0	A-C	A	R-0
5 to 30±	0	0	R-0	R-0	C	R-0	R-0	R-0
50 to 100±	0	0	--	0	R	0	0	0
SLASH-OPEN GROUND GROUP								
0 to 5±	R	R	R-0	0	A-C	A-C	A	0
5 to 30±	R	R	R	R	R	0	0	0
30 to 100±	R	R	--	R	R	R	R	R
CAVITY NESTING GROUP								
0 to 5±	0	R	R-0	R-0	0	R	R-0	0
5 to 30±	0	R	R-0	R-0	0	R	0	0
30 to 100±	0	R	--	R	0	R	0	0

of birds within the habitat groups may differ because of restricted geographic ranges or different proportions of conifers and hardwoods.

Uneven-Age Silviculture

A well-planned system of single tree or small group selection maintains an uneven-aged stand and, among harvest methods, comes closest to retaining a continuous cover of trees of many ages and heights. Vertical development is at a maximum (Frank and Bjorkbom 1973), which provides more canopy layers than any other silvicultural system. Horizontal diversity is maintained through a mosaic of different sites--resulting largely from glaciation--which form brushy bogs and swamps, blowdown openings, localized natural tree mortality, and localized type anomalies.

At short intervals, mature trees are removed as scattered individuals or small groups to provide a sustained yield of products, even from relatively small ownerships. Competing hardwoods and noncrop softwoods are thinned and weeded at the same time. The time between cuttings on a given area may range from 10 to 25 years, depending on the site and on economic considerations (Frank and Bjorkbom 1973). By frequent harvest cuts, trees that might otherwise die are cut, thus well-managed stands will not have as many standing dead trees.

Bird populations remain more stable with uneven-age than with even-age silviculture. Managed uneven-aged stands at any given time have a greater variety of habitat strata than unmanaged mature spruce stands. Numbers of bird species and densities of individuals would likely equal or exceed the levels found in the mature stands, although there would be fewer mature trees so the upper canopy would not support as many birds. The numbers of golden-crowned kinglets and blackburnian warblers would be less. However, the well-distributed canopies of the low and midstory trees should support more low canopy species such as the magnolia and yellow-rumped warbler, Swainson's thrush, and the solitary vireo, with an overall increase in numbers. Ground-feeding species such as the dark-eyed junco and white-throated sparrow will be found in small openings. Cavity nesters may be adversely affected.

Even-Age Silviculture

Harvest Cuttings

Clearcutting.--Silvicultural clearcutting is the felling of all stems greater than 2.5 to 5.0 cm in diameter at breast height (dbh). This type of cutting should be done only if advance reproduction or a seed source is available or if the area is to be replanted immediately. It is often advantageous to cut in small patches or narrow strips to facilitate natural seeding. Where environmental conditions are not too severe, the openings should be wider than one tree height and no wider than 25 to 30 m for balsam fir and 55 to 60 m for red and white spruce. Where there is danger of seedling dessication or wind damage, the openings should be no larger than half the height of the trees in the stand. Uncut areas should be at least 10 m wide (Frank and Bjorkbom 1973).

In the upland spruce-fir forest ecosystem, plant succession has five seral stages that follow severe disturbances such as clearcutting (Titterington et al. 1979), and each is characterized by one or more habitat feature: (1) open ground-slash--abundant open ground and dense slash; lasts from 0 to 2 years after disturbances; (2) bramble-herbaceous--dense low layer of brambles and herbaceous plants with scattered small regenerating tree species; lasts 3 to 10 years after disturbances; (3) shrub-sapling--dominated by hardwood and softwood regeneration taller than 2 m; lasts 4 to 20 years after a disturbance; (4) immature second growth--pole-size hardwoods and/or softwoods 10 to 20 cm dbh; lasts from 20 to 50 years after disturbances; (5) mature second growth--dominated by softwood > 20 cm dbh; lasts from 40 to 80 years after disturbances.

Avifaunal succession is directly related to these seral stages. Bird species that nest and forage predominantly on the ground, such as the white-throated sparrow, dark-eyed junco, and winter wren, are closely associated with the first seral stage. The slash commonly left after tree harvesting provides important protective cover for these bird species.

Bird species adapted to nest and forage in dense vegetation close to the ground are closely associated with the second seral stage. The white-throated sparrow, common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler, and mourning warbler (*Oporornis philadelphia*) all reach their highest densities in this habitat. The edges, with a dense growth of brambles, will also be used by these species.

Bird species, such as the white-throated sparrow, magnolia warbler, red-eyed vireo, American redstart (*Setophaga ruticilla*), and Canada warbler are abundant nesters and foragers in the dominant shrub-sapling stratum of the third seral stage. The white-throated sparrow and black-and-white warbler both nest on or near the ground, but spend a large part of their foraging time in saplings.

The substantial lower and midcanopies characteristic in the fourth seral stage provide abundant foraging sites for such species as the solitary vireo, Swainson's thrush, rose-breasted grosbeak (*Pheucticus ludovicianus*), black-throated blue warbler, Tennessee warbler, and the ovenbird. These last three species nest on or near the ground.

The dominant bird species of the fifth seral stage, such as the golden-crowned kinglet, yellow-rumped, black-throated green, bay-breasted, Cape May, and blackburnian warblers, satisfy their foraging and nesting requirements in the upper canopy.

Clearcutting for natural regeneration affects bird populations in proportion to the minimum size of stems cut and the size of areas cut. Upper and lower canopy habitats are eliminated with silvicultural clearcutting, but the understory is retained and a slash habitat may be created. Depending on site quality, in 2 to 4 years, the regenerating trees, herbs, and raspberries increase the understory density and provide habitat for the common yellowthroat, white-throated sparrow, and associated species. When stems 8 to 16 cm dbh are left uncut, some shrub-sapling and lower canopy birds such as the magnolia warbler and its associates will continue to find favorable habitat as will some cavity nesting species. However, this will lessen the understory growth with a resulting decrease in the number of understory birds. Site quality and subsequent thinning will determine the rate at which lower and upper canopies develop and provide habitat for canopy species.

Unlike large cleared areas, small clearcuts--from 2 to 8 ha (5 to 20 acres)--result in different aged stands and a greater variety of bird species found in close proximity at any one time. Long rotations, which result in increased crown development and stand size variety, enhance habitat for more bird species than short rotations regardless of the type of harvest system used in even-age silviculture.

Shelterwood.--Clearcutting small areas can be considered a shelterwood cut if the clearings are less than one-half the height of the trees in the stand. In shelterwood systems, a first harvest is made to establish reproduction and one or more later harvests remove the remaining stand when the regeneration no longer needs protection from wind and excessive insolation (Frank and Bjorkbom 1973).

Shelterwood methods cause the least drastic stand modification of the even-age silvicultural regeneration systems. When the overstory is removed in two or more operations at intervals of 5 to 25 years, the effects on birds are similar to group selection, especially if more than two cutting stages are used. When the last cut removes the remaining overstory, advanced reproduction is well established. Upper and lower canopy birds lose their habitat but shrub and sapling birds such as the magnolia warbler, and bramble-herbaceous birds such as the common yellowthroat, find improved habitat. Species such as the dark-eyed junco will be found in a dominant stratum of slash left after heavy cutting. The slash and shrub-sapling strata diminish with time as tree crowns increase in height and volume, which provides favorable conditions for low canopy species. Eventually the dominant trees again provide habitat favorable for both lower and upper canopy species. Cavity nesters would find little habitat after the final removal cut.

Planting and Seeding

Clearcutting followed by site preparation, planting, and control of competing vegetation causes the greatest disruption of upland spruce-fir stands.

Planting or seeding may be advantageous where natural regeneration is lacking or will take several years to develop, or where the better sites warrant planting superior stock. Competing vegetation and debris may be removed by mechanical means, chemical treatment, or controlled burning before planting or seeding. Generally these treated areas are substantially exposed.

The use of the area by birds would be inversely related to intensity of the practices employed. Heavy slash left in clearcut areas is used by dark-eyed juncos and winter wrens for foraging and nesting. Woodpeckers also forage in slash (Conner and Crawford 1974). When slash is eliminated, the area has little to attract these bird species.

If small seedlings are planted and competing vegetation is controlled, it may be 5 or more years before the area is suitable for species attracted to the shrub-sapling stratum. Depending on the amount of revegetation, some use of the area would probably be made by species such as the Savanna sparrow (*Passerculus sandwichensis*) that nest in open fields. Because plant succession is slower on poor sites, the length of time before shrub-sapling bird groups reoccupy the site may be longer than on better sites. For bird rehabitation, a favorable alternative would be closely spaced plantings of superior growing stock on better sites, with minimum vegetation control, and with slash left in place. The period of time that areas are unsuitable for birds would then be minimized.

Intermediate Cuttings

Even-age silvicultural systems require cultural treatments between harvest cuts to help the stand develop properly.

"Cleanings" done in sapling stands release and increase the growth of potential crop trees by removing nearby competing stems. Cleanings generally remove hardwood from spruce and fir on sites with deep, well-drained soils about 8 years after harvest. Cleanings may be done by cutting or by chemical treatment.

"Thinning" removes trees that compete with crop trees or those that may die before regeneration cuts are due, and speeds up the growth of the residual trees. It is conducted in pole-size and sawlog-size stands (Frank 1973). These cuts may remove 10 to 50 percent of the basal area, depending on the site.

After intensive thinning of hardwood and softwood species in pole-size spruce-fir stands, there is a decrease in use by upper canopy birds; removing softwood trees particularly affects nesting conditions. However, such thinning favors habitat use by lower canopy species.

Intensive thinning in sawlog-size stands releases hardwood understory and herbaceous ground cover, and increases use by shrub-sapling and lower canopy birds; upper canopy species continue to be represented. Continued growth of the hardwood understory creates favorable conditions for ovenbirds; black-throated green, black-throated blue, and Canada warblers; Swwinson's thrush; and rose-breasted grosbeaks. Cavity nesters are adversely affected by thinning such stands unless trees are killed and allowed to remain standing.

Intermediate cuttings decrease the number of hardwood trees in sapling spruce-fir stands during cleaning operations, which results in less use of the area by the black-and-white and Canada warblers, the red-eyed vireo, the American redstart, and associated species. If the weeding is intensive enough to cause a dense herbaceous growth, this benefits the common yellowthroat and associated species, and it might favor the dark-eyed junco and associated species if the hardwood slash is left.

Forest stands located on good sites respond to thinning more rapidly than stands on poor sites. Consequently, the alteration of habitat on good sites effects changes in bird species representation more quickly and for a shorter time.

Unregulated Methods

Commercial clearcutting and diameter-limit cutting usually remove the largest and best trees from a stand, which results in high grading. The size and quality of stems harvested are usually determined by marketing conditions. These cutting methods are not designed to provide regeneration, but may do so; neither do they generally provide for any cultural treatments. Intensity of harvest may vary from light removal of large trees from old-growth stands to removal of all spruce and fir except culls and saplings.

Large diameter limit harvests do not maintain a proper distribution of tree size classes through thinning. Vertical canopy development would not be as great as in managed uneven-aged stands. Distribution of trees in the lower canopy would be left to chance and the number and density of bird species would be correspondingly less than in managed uneven-aged stands. Habitat for cavity nesters would be favorable because cull trees are left standing.

Small diameter limit cuts and commercial clearcutting open the stand to varying degrees depending on the number of saleable trees. This cutting does not remove stems in the lower size classes, and shrub-sapling and low canopy strata usually are not reduced. Many birds frequenting these habitats remain, or possibly increase, due to increased vegetative growth. If understory vegetation is poorly developed, stands are of less value to birds. Noncommercial or cull overstory trees are left which provide a variable amount of habitat for upper canopy species. Habitat for cavity nesters can be favorable.

SUMMARY

Five seral stages with corresponding bird species succession follow severe disturbance in upland spruce-fir forests:

(1) Open ground-slash--white-throated sparrow, dark-eyed junco, and winter wren.

(2) Bramble-herbaceous--white-throated sparrow, common yellowthroat, chestnut-sided warbler and associates.

(3) Shrub-sapling--white-throated sparrow, magnolia warbler, red-eyed vireo and associates

(4) Immature second growth--solitary vireo, Swainson's thrush, black-throated blue warbler and associates.

(5) Mature second growth--golden-crowned kinglet, blackburnian warbler, yellow-rumped warbler and associates.

In forest stands, the composition and density of bird communities is affected by the admixture of hardwoods with softwoods, vertical and horizontal stand structure, and degree of spruce budworm infestation in the stands. Based on number of bird species present and population density, we separated forest stands as follows:

Stand	Pairs/40 ha	No. species
Balsam fir	128	20
Mature spruce	264	23
Mixed growth	231	24
Spruce-fir w/budworm	334	34
Spruce-fir no budworm	190	26
Young spruce	249	17

Silvicultural practices modify stands by changing plant composition and vertical and horizontal stand structure. To meet their nesting and foraging requirements, bird populations respond by utilizing the habitat to which they are best adapted.

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BIRD COMMUNITIES ASSOCIATED WITH SUCCESSION AND MANAGEMENT OF LOWLAND CONIFER FORESTS

Deanna K. Dawson[1]

Abstract.--Data from published bird censuses were used to determine changes in avian communities in relation to plant succession, fire, type conversion, and timber management practices in lowland conifer forests in the northeastern United States. With modifications in current logging practices, habitat for the bird species that nest in undisturbed stands can be provided. Management guidelines are recommended.

INTRODUCTION

Lowland conifer forests comprise over five million acres of the commercial forestland in the northeastern United States, and an even larger area of the type has been classified as noncommercial because of stunted and sparse timber growth. This paper deals with the northern lowland conifer communities, in which tamarack (Larix laricina), black spruce (Picea mariana), or northern white-cedar (Thuja occidentalis) are dominant. These forests have long been of interest to botanists because of the presence of insectivorous plants and numerous species of orchids, but the avian communities have received much less attention. Communities of birds associated with different successional stages will be identified, and guidelines will be discussed for making timber management practices compatible with the maintenance of avian habitat. Other lowland conifer species not considered here are Atlantic white-cedar (Chamaecyparis thyoides) which grows in a narrow belt along the Atlantic coast as far north as southern Maine, and loblolly pine (Pinus taeda) which grows on the Coastal Plain and Piedmont from Delaware south.

METHODS

Little study has been conducted on avian populations in lowland conifer stands. In order to identify the bird species associated with different successional stages, I drew together information from several sources. For information on species abundance, I relied mainly on Breeding Bird Censuses conducted in the northeastern United States and Canada (Audubon Field Notes 1959-1970; American Birds 1971-1977) and on other studies which used the same census technique (International Bird Census Committee 1970). These include studies by Brewer (1967), Kendeigh (1948), Martin (1960), Stewart and Aldrich (1952), and a study in progress on the Seney National Wildlife Refuge in Upper Michigan by the Migratory Bird and Habitat Research Laboratory, USDI Fish and Wildlife Service. Censused plots were grouped into six different lowland communities following Erskine (1977). Density figures were calculated based on the mean number of territorial males per 40 hectares on plots where each species was recorded. I also referred to regional references on birds, such as Roberts (1932) and Palmer (1949), and read the chapters in Bent's life history series (Bent 1937, 1938, 1939, 1942, 1953, 1968) to fill in when information on a species was scant. Since no density figures were available, I evaluated only whether these species would commonly be found. All these sources were also used as the basis for determining the effect of timber management practices on birds.

THE LOWLAND CONIFER FORESTS

Most of the lowland conifer forests in the northeastern United States are growing on organic soils or peat. Some of these peatlands have developed with the buildup of encroaching vegetation in small lakes and depressions left by glacial activity. Sedges and sedgelike plants grow toward the center of the basin from the shore, forming a floating mat of vegetation. Other peatlands formed with the accumulation of reed-sedge debris in poorly drained glacial lakebeds. The bog community becomes established as sphagnum moss

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and ericaceous shrubs invade the sedge mat. Tamaracks are generally the first trees to appear, and peat compressed by the weight of the sphagnum and increased shrub growth also provides a favorable seedbed for black spruce. With continued buildup of organic material and a lowering of the water table, a dense spruce forest can develop. If the peat has become consolidated and firm, northern white-cedar may slowly invade the lowland conifer forest.

The young cedars that become established can spread by vegetative reproduction, and eventually can prevent shrub growth and further regeneration of tamarack and black spruce. In most cases, shade-tolerant balsam fir (*Abies balsamea*) is the only other tree species to become established (Curtis 1959, Johnston 1972, Martin 1959). White pine (*Pinus strobus*) and deciduous species are found growing with northern white-cedar in the transition to uplands. The range of the lowland conifer species is shown in Figure 1. In the southernmost parts of the range, tamarack occurs in pure stands or in association with lowland hardwood species such as red maple (*Acer rubrum*).

Common Plants of the Open Bog

Shrubs

- Bog birch (*Betula pumila* and *glandulosa*)
- Bog laurel (*Kalmia polifolia*)
- Bog rosemary (*Andromeda glaucophylla*)
- Cranberry (*Vaccinium macrocarpon*)
- Labrador Tea (*Ledum groenlandicum*)
- Leatherleaf (*Chamaedaphne calyculata*)

Herbs

- *Bladderwort (*Utricularia* sp.)
- *Pitcherplant (*Sarracenia purpurea*)
- *Round-leaved sundew (*Drosera rotundifolia*)
- Cottongrass (*Eriophorum angustifolium*)
- Bog buckbean (*Menyanthes trifoliata*)
- **Arethusa (*Arethusa bulbosa*)
- **Grass pink (*Calopogon pulchellus*)
- **Rose pogonia (*Pogonia ophioglossoides*)

* insectivorous plants ** orchid species

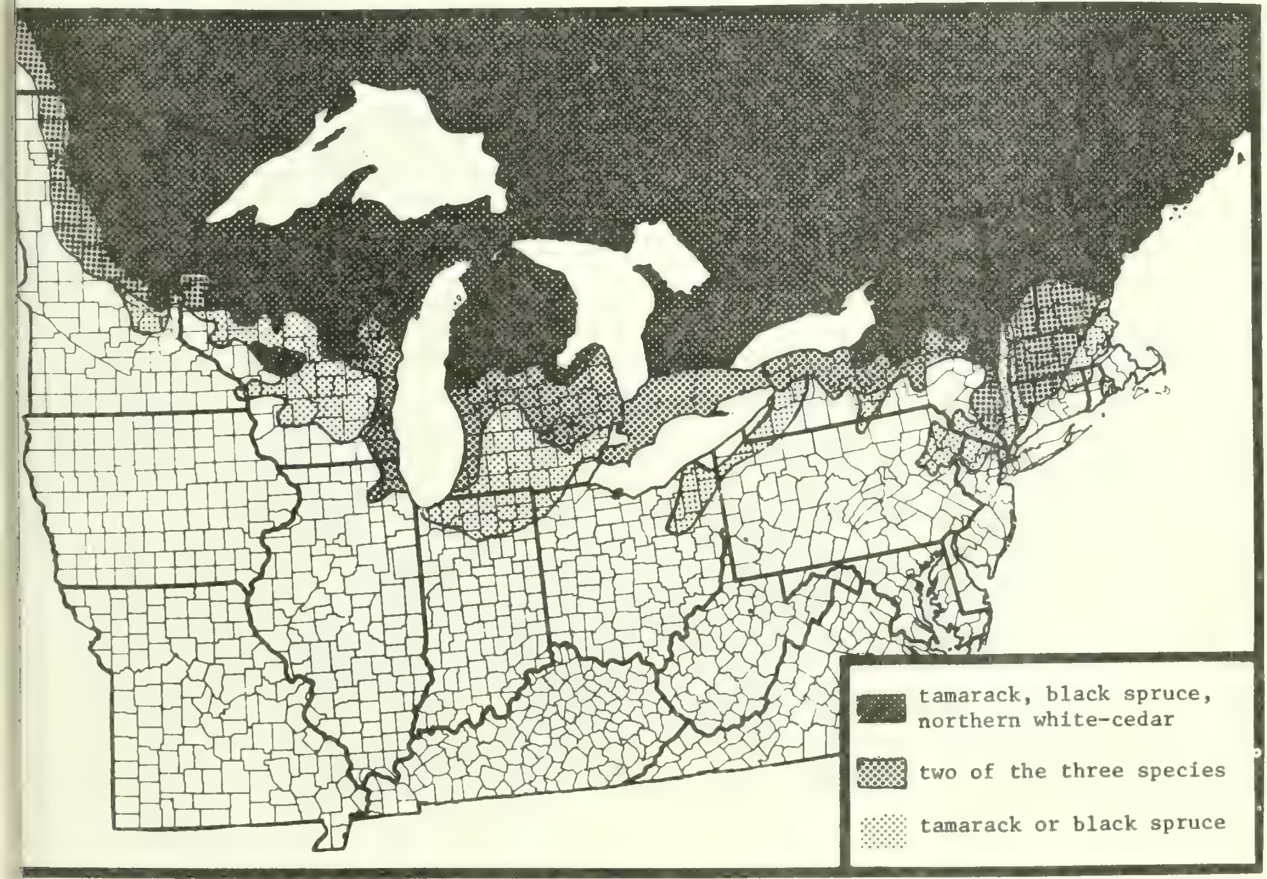
▓ tamarack, black spruce, northern white-cedar
▒ two of the three species
░ tamarack or black spruce

Figure 1.--Ranges of the northern lowland conifer forest species in the Northeastern United States. All species also occur farther south in isolated areas of the Appalachian Mountains and throughout most of Canada (Little 1971).

BIRDS OF LOWLAND CONIFER COMMUNITIES

Breeding birds of six different lowland conifer communities are shown in Table 1.[2] Several species (designated with an asterisk) are only locally common (such as the Gray Jay and Northern Waterthrush) and may be found in high densities in some areas but absent in similar habitat within their breeding range. The breeding ranges of other species (e.g. Wilson's and Palm Warblers) extend southward only to the northernmost United States, and consequently these birds will not be present in most lowland conifer stands. Differences in breeding ranges also account for the absence of Connecticut Warblers in bogs in New England and Blackpoll Warblers in mature spruce forests in the North Central states. Other species have specific habitat requirements that preclude their nesting in most stands. Sharp-tailed Grouse have only been found in the extensive areas of open bog and scattered low conifers (Hanson 1953), such as those in northern Minnesota or Upper Michigan. Savannah Sparrows are common only in bogs with large open patches of grasses and sedges.

Although several species, such as the Spruce Grouse, Yellow-bellied Flycatcher, Palm Warbler, Northern Waterthrush, and Lincoln's Sparrow, are more common and reach higher densities in these habitats, neither these nor any other characteristic species are unique to these forest types. Birds of the open bog-shrub community can also be found nesting in alder thickets or in the shrubby growth along lakes and streams. Likewise, a mature black spruce stand has an avian community similar to an upland spruce-fir forest.

The avian community of a stand in which tamarack is dominant includes bird species common in shrubby areas as well as species generally associated with hardwood forests. Tamarack, though a conifer, is deciduous; during late fall and early spring when needles are absent, the increased sunlight reaching the forest floor stimulates shrub growth. Even during the summer months, the fine needles and relatively open canopy cast little shade, so that mature tamarack stands generally have a much denser understory than mature spruce or white-cedar forests. At the time many of the birds are arriving in the spring, tamarack swamps resemble hardwood forests more than lowland conifer stands. Though few northern white-cedar stands have ever been censused, high densities of Northern Parulas and Black-throated Green Warblers make the avian community distinct.

If trees are killed by fire, high water, insects, or disease, woodpeckers and Brown Creepers may come in to forage for insects on snags and downed timber. The Black-backed Three-toed Woodpecker in particular is likely to be found in areas in which there are many standing dead trees. In addition, there are twenty species of birds that may nest in cavities in dead or dying trees.

Cavity-nesting Birds of Northern Bogs and Coniferous Forests

Common Goldeneye
Common Merganser
Red-breasted Merganser
Hooded Merganser
American Kestrel

Saw-whet Owl
Yellow-shafted Flicker
Pileated Woodpecker
Yellow-bellied Sapsucker
Hairy Woodpecker
Downy Woodpecker
Black-backed Three-toed Woodpecker
Northern Three-toed Woodpecker
Great Crested Flycatcher
Tree Swallow
Black-capped Chickadee
Boreal Chickadee
Red-breasted Nuthatch
House Wren
Starling

During outbreaks of insect pests, populations of certain bird species have been shown to increase. Though the spruce budworm (*Choristoneura fumiferana*) mainly attacks balsam fir and white spruce (Picea glauca), it can maintain itself over a period of years on black spruce (Blais 1957). Kendeigh (1947) and Morris *et al*. (1958) reported strong increases in densities of several warbler species, particularly the Bay-breasted and Tennessee Warblers, in response to outbreaks of the spruce budworm in spruce-fir forests. Buckner and Turnock (1965) found the fringillids (grosbeaks, finches, and sparrows) to be more important than the warblers as predators of the larch sawfly (*Pristiphora erichsonii*) in tamarack bogs. Small flocks of nonresident avian species were also observed foraging in areas of high sawfly densities.

Though few hawks and owls have been recorded in censuses of lowland conifer stands, several species of raptors do nest in and use these habitats. Roberts (1932) reported nesting of the Sharp-shinned Hawk, Broad-winged Hawk, Great Horned Owl, and Long-eared Owl in conifer swamps in Minnesota. The few nesting records of the Great Gray Owl in the northeastern United States have been in tamarack bogs (Roberts 1936, Nero 1970), and Nero *et al*. (1974) also reported the successful occupancy by this species of an artificial nest placed in a tamarack tree. Keran (1978) pointed out the need for a variety of habitat types by nesting Broad-winged Hawks. Although oak-aspen was the preferred forest type, the presence of a wet area and some type of upland

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[2] Scientific names in Appendix.

Table 1.--Abundance of breeding bird species found in various stages of lowland conifer succession.[1]

Bird Species	Dominant Plants					
	Open bog-low shrubs (4)[2]	Shrubs, scattered conifers (13)	Young or low Black Spruce (2)	Medium-mature B.Spruce (5)	Tamarack (3)	Northern White-cedar (3)
American Bittern	U[3]					
Sora	U					
Killdeer	U	+				
Mallard	U	+				
Black Duck	2	+				
*Sharp-tailed Grouse	U	U				
Marsh Hawk	U	U				
American Goldfinch	U	6				
Common Snipe	C	+				
Eastern Kingbird	[illegible]	+				
Red-winged Blackbird	7	2				
Savannah Sparrow	C	6				
Lincoln's Sparrow	C	12	+			
Swamp Sparrow	133	15			4	
Song Sparrow	21	35			53	+
Common Yellowthroat	87	19	15	2	39	+
Alder Flycatcher	2	6			4	
Rufous-sided Towhee	U	14			17	+
Chestnut-sided Warbler	U	5	U	2	U	1
Palm Warbler		6	5			
American Robin		4	U	+	11	3
Canada Warbler		53	U	6	6	50
Cedar Waxwing		8	4	6	3	1
Hermit Thrush		5	5	3	C	+
Slate-colored Junco		[illegible]	6	2	C	+
Nashville Warbler		19	4	13	28	14
Myrtle Warbler		3	5	12	U	7
White-throated Sparrow		14	7	15	60	21
*Northern Waterthrush		77	9	2	4	+
Ruby-crowned Kinglet		2	15	11	C	7
Magnolia Warbler		1	7	14	C	
Boreal Chickadee		1	U	4		
Swainson's Thrush		+	4	7	U	33
Chipping Sparrow		2	U	8	3	1
Winter Wren		5	U	3	1	11
Blackburnian Warbler		7	2	2	U	[illegible]
Black-and-white Warbler		+	2	4	2	10
Olive-sided Flycatcher		+	U	2	U	+
*Tennessee Warbler		U		12	U	37
*Blackpoll Warbler		37	U	U	U	U
Purple Finch		4	2	1	1	2
Yellow-bellied Flycatcher		3	U	2		24
Spruce Grouse		+	U	2		
*Gray Jay		+	2	2		
*Connecticut Warbler		U	U			
*Wilson's Warbler		+	+			
*Rusty Blackbird		2				
Golden-crowned Kinglet			8	6		9
Red-breasted Nuthatch			U	7	1	2
Cape May Warbler			U	16		
Blue Jay				5	3	3
Ovenbird			U	30	14	17
*Evening Grosbeak				U	U	U
Pine Siskin			U	2		
White-winged Crossbill			U	4		1
Brown Creeper				2	2	9
Veery				6	47	+
Northern Parula				U	U	23
*Bay-breasted Warbler				2		37
Ruffed Grouse					3	1
Rose-breasted Grosbeak					9	1
American Woodcock					3	+
Eastern Wood Pewee					+	4
Wood Thrush					+	2
Scarlet Tanager					+	2
Black-throated Green Warbler						26

[1] Bent 1937, Bent 1938, Bent 1939, Bent 1942, Bent 1953, Bent 1968, Bond 1959, Brewer 1967, Bridge and Bridge 1964, Brunton and Crins 1975, Chapman 1907, Erskine 1977, Hall 1961-1963, Kendeigh 1948, Linehan 1968; Loery 1966, 1969-1970; Martin 1960, Palmer 1949, Roberts 1932, Root 1942, Speirs and Orenstein 1975, Stewart and Aldrich 1952; Van Velzen 1972-1974, 1977.

[2] Number of censuses.

[3] Mean density per 40 hectares on plots where species was recorded. When density figures were not available, C = common, U = uncommon.
+ denotes presence on plot, but no established territory was determined.

* locally common

opening seemed a requirement for nest-site selection. In a study of four species of raptors (Broad-winged Hawk, Red-tailed Hawk, Barred Owl, and Great Horned Owl), Fuller (1979) found differential habitat use between individuals of the same species. White-cedar and tamarack swamps made up over 26% of the total home range and over 18% of the total detected locations of a female Barred Owl; another radioed female used tamarack in proportion to its availability. However, since lowland conifers made up a much smaller percentage of her home range (only 2%), use of upland types was significantly higher for this bird. He also reported changing habitat use and preference by individuals as home range shifted to new areas and different habitats occurred within the range. He attributed this shifting of habitat use to resource availability and potential competition with other species of raptors. Of the species studied, only the Red-tailed Hawk did not use lowland areas extensively. Although lowland conifer stands may not be preferred for nesting habitat, they may be important to this group of birds for other activities and at other times of the year. Forbes and Warner (1974) found a northern white-cedar swamp to be the preferred roosting habitat of a radioed Saw-whet Owl in central Minnesota. Tamarack swamps were most used by this species during winter in a study in Michigan (Mumford and Zusi 1958).

Winter populations of birds in lowland conifer stands vary with the seed crop. Black spruce trees bear seeds as early as ten years of age and become dependable producers, with heavy crops occurring about every four years (USDA Forest Service 1965). In addition, seeds are shed slowly and throughout the year. In good seed years or when seed crops are low elsewhere, an influx of northern finches (Pine Grosbeak, Pine Siskin, Red Crossbill, White-winged Crossbill) is not uncommon in black spruce stands. In contrast, nearly 98% of the tamarack seed crop in northeastern Minnesota was reported to fall before the end of October (Duncan 1954). Likewise, most of the seeds of northern white-cedar are dispersed by November (USDA Forest Service 1965). Even in heavy seed years, these species do not provide a good food source; birds present in winter in stands where tamarack or northern white-cedar are dominant are likely to be limited to permanent residents. The grouse, owls, woodpeckers, jays, chickadees, siskins, and crossbills do winter in northern forests.

FACTORS AFFECTING STAND COMPOSITION AND AVIAN COMMUNITIES

Fire

During periods of drought, the surface layers become dry enough to make bogs and swamps susceptible to fire. If the burn is light, the bog community will become reestablished when water levels return to normal (Curtis 1959). However, if the upper layers of peat are destroyed, an open bog-sedge meadow community may develop, with a mixture of leatherleaf and sedges growing in a loose sphagnum mat (Curtis 1959, Vogl 1964). This type of area may attract Savannah Sparrows which would not ordinarily be found in a bog with heavy shrub cover.

Although the lowland conifers are not resistant to fire, all reproduce well on burned organic soils if seed-bearing trees are nearby. Many of the extensive acreages of even-aged black spruce or white-cedar swamp and forest in the Lake States originated after fire (Curtis 1959). If the burned peat is dry enough however, paper birch (Betula papyrifera) and quaking aspen (Populus tremuloides) are likely to become established, making the successional pattern similar to that after fire on upland sites. These hardwoods, shrubs, and other competing vegetation will overtop many of the conifer seedlings and slow their growth, but, except on the best sites, the conifers will eventually become dominant. The results of a census conducted on the Seney National Wildlife Refuge[3] show the bird species present on an 8 hectare burned black spruce plot with many snags. Cape May and Magnolia Warblers, Ovenbirds, and Golden-crowned Kinglets, all present in a mature black spruce forest nearby, were not found in the burned stand.

Breeding Birds of a Burned Spruce Forest
Seney National Wildlife Refuge, 1978[3]

	# territorial males per 40 ha*
White-throated Sparrow	30
Chipping sparrow	25
Slate-colored Junco	15
American Robin	10
Myrtle Warbler	10
Nashville Warbler	7
Black-backed Three-toed Woodpecker	5
Winter Wren	5
Brown Creeper	2
Killdeer	+
Hairy Woodpecker	+
Lincoln's Sparrow	+

*actual counts expanded to be comparable with densities in Table 1.

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[3] Unpublished data, U.S. Fish & Wildlife Service.

Type Conversion and Peat Mining

During the late 1800's and early 1900's, many of the southernmost conifer swamps were drained for conversion to agricultural crops (Curtis 1959). Similar attempts were made farther north, but the harsher climate made agricultural ventures largely unsuccessful.

The extensive bogs and swamps of the Lake States are again receiving attention with the interest in the use of peat as an energy source. Peat has been mined on a small scale for years, mainly for horticultural purposes, with the northern Lake States accounting for over 40% of the total produced in the United States in 1977 (USDI Bureau of Mines 1978). Current research is focusing on the feasibility of mining peat on a much larger scale for conversion to a synthetic natural gas or for direct use as a fuel. If some of these peatlands are to be developed, guidelines for reclamation would have to be established and unique natural areas identified and preserved. Finland has been successfully using reclaimed peatlands for forestry purposes; production of forage and seed crops, cool season grasses and vegetables, or wild rice is also being considered on former peatland (Farnham 1978).

Mining and the resulting conversion to another vegetation type would undoubtedly have a great impact on birds. These activities would center in the peatlands where disturbance has been minimal in the past--those that do not produce merchantable timber, and, because of high water tables and unstable terrain, have received little recreational use.

Timber Management Practices

Though much of its acreage is classified as noncommercial, the lowland conifer type represents 13% of the total commercial forestland in the northern Lake States and nearly 5% of the commercial forestland in the New England states and New York (Kingsley 1976, Kingsley 1977, Peters and Bowers 1977, Spencer and Thorne 1972, Ferguson and Mayer 1970, Ferguson and Kingsley 1972). Black spruce and tamarack are cut as pulpwood where stands are large enough to make logging profitable, and white-cedar is harvested for use as posts, poles, and lumber products where its resistance to decay is of prime importance.

Harvesting and Site Preparation

Clearcutting is the recommended method for harvesting and reproducing the lowland conifers (Johnston 1977a,b; Heinselman 1959). Black spruce and tamarack reproduce best in full sunlight, and wind damage to these shallow-rooted species is minimized in the resulting even-aged stands. Northern white-cedar is highly preferred by white-tailed deer (Odocoileus virginianus) for winter shelter and browse, and timber management practices have in the last decade been influenced by their need for large, dense even-aged stands in traditional yarding areas (Verme 1965).

Cutting of cedar is generally done in strips or small blocks, leaving alternate rows of the same width for a seed source. Clearcut strips can vary in width from 1 chain (~20 meters) to 3 chains, depending on the height of trees in the adjacent uncut stands (Johnston 1977b). After the cutover areas are restocked (usually within 10 years), the uncut strips should be logged to prevent the new stands from becoming over-seeded and to reduce overbrowsing of the reproduction in the clearcuts by deer. Generally, shelterwood cuts are recommended at this point to ensure a seed source for the newly logged areas (Johnston 1975, 1977b). In most cases, however, this followup is not done, and the uncut strips remain. Black spruce and tamarack stands are cut either in strips or in large blocks, usually 40 acres (~16 hectares) or greater (Johnston 1977, Duncan 1952). If broadcast-burning of the cutover area is needed to improve the seedbed, to control disease, or to remove brush and undesirable residual stems, block cutting is more economical and preferred. However, since natural seeding cannot be relied on further than about 260 feet (~80 meters) from mature trees (Johnston 1975), direct seeding is usually required with this harvest method. Strip cutting is best applied in large stands that do not require broadcast-burning.

Clearcut-logging sets the vegetation of a stand back to an earlier successional stage. The avian communities will revert likewise, with bird species associated with open shrubby areas replacing those which nested in the mature forests (see Table 1). Unfortunately, the study of birds in lowland conifer communities has been confined almost entirely to natural stands; hence there is little documentation of avian use of logged areas. It does seem evident that species composition and densities will vary with the treatment after logging.

Black spruce, tamarack, and northern white-cedar reproduce best where slash cover is minimal. Burning is generally the recommended method for disposing of heavy slash, but, particularly in small cuts, full-tree skidding is less expensive and most often practiced (Johnston 1977a,b). Stands harvested by full-tree skidding or broadcast-burned following logging will not attract as many birds as cuts in which more slash is left. With little or no slash, Brewer's

Blackbirds and Common Yellowthroats are probably the most likely species to nest in a recently logged area. The bird species present on a lowland plot on Seney National Wildlife Refuge in Upper Michigan[4] censused by the spot-mapping method (Williams 1936) are shown below. Though actually altered by fire, the vegetation structure of this plot is very similar to that of a clearcut-logged area with heavy slash, with toppled trees and a few standing snags. In addition, Winter Wrens may be attracted to brush piles along the edge of a clearcut. Other species, though nesting elsewhere, will feed in snags and among the slash, or take advantage of the openings created by logging for hunting or flycatching.

Breeding Birds of a Burned Tamarack Forest
Seney National Wildlife Refuge, 1978[4]

Yellow-shafted Flicker
Tree Swallow
American Robin
Nashville Warbler
Common Yellowthroat
Brewer's Blackbird
White-throated Sparrow
Lincoln's Sparrow
Song Sparrow

Intermediate Treatment

On good sites, growth of deciduous brush (alder, dogwood, etc.) may severely suppress the conifer reproduction (Johnston 1977a,b). Aerial herbicide spraying is currently the most commonly used method of killing overtopping shrubs and hardwoods, despite the greater risk in lowland areas of contaminating open water. More research is being done (Johnston 1973) to determine if different broadcast-burning methods (season and severity) will sufficiently control shrub growth. Stands that are brushy will attract more species and have higher densities of birds than non-brushy stands or stands where shrub growth has been controlled. Sites allowed to revert to lowland brush may even attract species more common in upland deciduous clearcuts, such as the Chestnut-sided and Golden-winged Warblers.

In older stands of northern white-cedar, thinning improves both timber quality and deer habitat. Because the canopy closes gradually after thinning, stands must be rethinned periodically to maintain enough light for advance tree reproduction to continue growth (Johnston 1972). In these stands and in those which are understocked or have been direct-seeded, Ruby-crowned Kinglets, Magnolia Warblers, Myrtle Warblers, and Slate-colored Juncos will probably be common bird species. Blackburnian Warblers, Ovenbirds, Cape May Warblers, and Golden-crowned Kinglets are likely to be found breeding in the densest stands.

To ensure that northern white-cedar will remain dominant in the next stand, preparatory treatment, 5 to 10 years before harvesting, is recommended where intensive management for timber or deer habitat can be justified (Johnston 1977b). Hardwoods and undesirable trees are generally cut if they are merchantable, but girdling and application of herbicide are also used to kill these trees and control their vegetative reproduction. If cutting of these hardwoods creates an opening in the forest, shrub growth may increase and provide habitat for a bird species, such as the Nashville Warbler, not normally found nesting in the forest interior. Snags left by girdling or herbicide treatment may be used as avian nesting and feeding sites.

Rotation Age

Growth rates of lowland species vary tremendously with site. The best sites have moderately well decomposed woody peat and occur where the soil water is continuous with the ground water system and enriched by nutrients from areas with mineral soil (Johnston 1977a,b). The growth rates for tamarack and black spruce are poorest in open bogs, where site fertility is almost totally dependent on precipitation. White-cedar particularly requires actively moving soil water and, in lowland areas, it achieves its maximum growth rate along streams or drainage ditches (Johnston 1977b).

Though site, stocking, and the presence or risk of wind damage and disease may determine the actual harvest age, the recommended rotation for black spruce generally does not exceed 100 years, because butt rot becomes common thereafter on organic soils (Johnston 1977a). A rotation range of from 70 to 160 years has been established for white-cedar (Johnston 1977b), depending again on site and on the desired timber product. Stands managed to maximize board feet (110 years and older) provide optimum winter shelter for deer (Johnston 1977b) and also provide more years of available habitat for birds associated with mature forests. There is no information available on the minimum area of contiguous forestland required by these species. However, study being conducted in the Eastern deciduous forests (Whitcomb et al. 1979) indicates that certain bird species will no longer be present as forests are fragmented into small areas.

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[4] Unpublished data, U.S. Fish & Wildlife Service.

In general, treatment and succession following logging provide breeding habitat for the bird species that nest in natural lowland conifer stands. Species associated with relatively open bog areas with only scattered trees, such as the Palm Warbler, probably will not find cutover areas and the resulting stands suitable; their prime nesting habitat is generally in the extensive acreages of lowland conifers classified by foresters as noncommercial and little of this habitat is altered by logging activities. However, birds normally associated with shrubs, such as the Common Yellowthroat, Swamp Sparrow, and Song Sparrow, are wide-ranging and seem partial to the shrub vegetation form; hence they will find suitable growth in logged as well as undisturbed habitats. Populations of some species, such as the Nashville Warbler, may rise with the increase in the amount of edge between mature and young growth created by logging. Provided that large blocks of forest remain uncut, the recommended rotation age and the usual reliance on adjacent stands as the seed source for cutover areas ensures the presence of habitat required by bird species associated with mature conifers.

SUMMARY AND RECOMMENDATIONS

Since birds assist in controlling insect populations, and with the increased enthusiasm for recreational birding and the greater appreciation of nongame species as part of the ecosystem, the land manager should develop some guidelines for increasing bird habitat. With modifications in current logging practices, habitat for more species and greater densities of birds can be provided. Some recommendations for management follow.

1. Timber sales should be planned so as to maintain large blocks of mature forests. If strip cutting is to be used, the width of uncut strips should be increased, particularly if a followup cut is not anticipated.

2. As often as possible, rotation cycles should be lengthened to provide more years of available habitat for birds requiring mature forests.

3. A few snags and live trees should be left standing in a clearcut. Snags provide nesting and feeding sites for many bird species and are also good perches for raptors hunting in the openings created by logging.

4. Some slash should be left in a clearcut to increase bird use in the first growing season after logging.

5. If direct seeding is to be used to establish second growth, openings should be left where shrub growth would not need control.

6. Brush control should not be used unless the young conifers definitely need release. If herbicides are to be used, application late in the summer will reduce the chances of interference with nesting.

7. In the recommended thinning and preparatory treatment for northern white-cedar, undesirable trees should be girdled and not cut.

8. More information about avian use of lowland conifer habitats would be valuable. Research is especially needed on how bird communities change during the successional stages following logging.

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APPENDIX

Scientific Names of Bird Species

Ducks through Owls

allard	Anas platyrhynchos
lack Duck	Anas rubripes
ommon Goldeneye	Bucephala clangula
ommon Merganser	Mergus merganser
ed-breasted Merganser	Mergus serrator
ooded Merganser	Lophodytes cucullatus
harp-shinned Hawk	Accipiter striatus
arsh Hawk	Circus cyaneus
ed-tailed Hawk	Buteo jamaicensis
road-winged Hawk	Buteo platypterus
merican Kestrel	Falco sparverius
pruce Grouse	Canachites canadensis
uffed Grouse	Bonasa umbellus
harp-tailed Grouse	Pedioecetes phasianellus
merican Bittern	Botaurus lentiginosus
ora	Porzana carolina
illdeer	Charadrius vociferous
merican Woodcock	Philohela minor
ommon Snipe	Capella gallinago
reat Horned Owl	Bubo virginianus
ong-eared Owl	Asio otus
arred Owl	Strix varia
reat Gray Owl	Strix nebulosa
aw-whet Owl	Aegolius acadicus

Woodpeckers

ellow-shafted Flicker	Colaptes auratus
ileated Woodpecker	Dryocopus pileatus
ellow-bellied Sapsucker	Sphyrapicus varius
airy Woodpecker	Picoides villosus
owny Woodpecker	Picoides pubescens
lack-backed Three-toed Woodpecker	Picoides arcticus
orthern Three-toed Woodpecker	Picoides tridactylus

Flycatchers and Swallows

astern Kingbird	Tyrannus tyrannus
reat Crested Flycatcher	Myiarchus crinitus
ellow-bellied Flycatcher	Empidonax flaviventris
lder Flycatcher	Empidonax alnorum
astern Wood Pewee	Contopus virens
live-sided Flycatcher	Nuttallornis borealis
ree Swallow	Iridoprocne bicolor

Jays through Creepers

lue Jay	Cyanocitta cristata
ray Jay	Perisoreus canadensis
lack-capped Chickadee	Parus atricapillus
oreal Chickadee	Parus hudsonicus
ed-breasted Nuthatch	Sitta canadensis
rown Creeper	Certhia familiaris

Wrens through Starlings

House Wren	Troglodytes aedon
Winter Wren	Troglodytes troglodytes
American Robin	Turdus migratorius
Wood Thrush	Hylocichla mustelina
Hermit Thrush	Hylocichla guttata
Swainson's Thrush	Hylocichla ustulata
Veery	Hylocichla fuscescens
Golden-crowned Kinglet	Regulus satrapa
Ruby-crowned Kinglet	Regulus calendula
Cedar Waxwing	Bombycilla cedrorum
Starling	Sturnus vulgaris

Warblers

Black-and-white Warbler	Mniotilta varia
Golden-winged Warbler	Vermivora chrysoptera
Tennessee Warbler	Vermivora peregrina
Nashville Warbler	Vermivora ruficapilla
Northern Parula	Parula americana
Magnolia Warbler	Dendroica magnolia
Cape May Warbler	Dendroica tigrina
Myrtle Warbler	Dendroica coronata
Black-throated Green Warbler	Dendroica virens
Blackburnian Warbler	Dendroica fusca
Chestnut-sided Warbler	Dendroica pensylvanica
Bay-breasted Warbler	Dendroica castanea
Blackpoll Warbler	Dendroica striata
Palm Warbler	Dendroica palmarum
Ovenbird	Seiurus aurocapillus
Northern Waterthrush	Seiurus noveboracensis
Common Yellowthroat	Geothlypis trichas
Connecticut Warbler	Oporornis agilis
Wilson's Warbler	Wilsonia pusilla
Canada Warbler	Wilsonia canadensis

Blackbirds and Tanagers

Red-winged Blackbird	Agelaius phoeniceus
Rusty Blackbird	Euphagus carolinus
Brewer's Blackbird	Euphagus cyanocephalus
Scarlet Tanager	Piranga olivacea

Finches and Sparrows

Rose-breasted Grosbeak	Pheucticus ludovicianus
Evening Grosbeak	Hesperiphona vespertina
Purple Finch	Carpodacus purpureus
Pine Grosbeak	Pinicola enucleator
Pine Siskin	Spinus pinus
American Goldfinch	Spinus tristis
Red Crossbill	Loxia curvirostra
White-winged Crossbill	Loxia leucoptera
Rufous-sided Towhee	Pipilo erythrophthalmus
Savannah Sparrow	Passerculus sandwichensis
Slate-colored Junco	Junco hyemalis
Chipping Sparrow	Spizella passerina
White-throated Sparrow	Zonotrichia albicollis
Lincoln's Sparrow	Melospiza lincolnii
Swamp Sparrow	Melospiza georgiana
Song Sparrow	Melospiza melodia

THE ECOLOGY AND MANAGEMENT OF AVIAN COMMUNITIES IN MIXED HARDWOOD-CONIFEROUS FORESTS

Stanley A. Temple[1], Michael J. Mossman[2], and Bruce Ambuel[2]

Abstract.--High horizontal diversity of vegetation in mixed hardwood-coniferous forests is identified as a key feature affecting avian communities. The extremely high bird species diversity of mixed forests is explained by patchiness of forest vegetation and selection of discrete habitat patches by birds that are typical of either more northerly or southerly forest types. Bird population densities, seasonality of avian communities, and impacts of succession on avian communities are interpreted in relation to forest ecology. Impacts of silviculture on avian communities are predicted, and modifications that favor diverse avian communities are suggested.

INTRODUCTION

In spite of their northerly distribution, the various types of mixed hardwood-coniferous forests in north central and northeastern United States support remarkedly rich avifaunas. The bird species diversities in these mixed forest types are among the highest of any of the forests in North America and the highest of any of the forest types in the north central and northeastern regions (Table 1). This conspicuously high bird species diversity provides the basis for our discussion of the bird communities of the mixed forests. We address ourselves to the following questions: What characteristics of the forest vegetation allow such diverse bird communities to develop? How do the geographic distributions and habitat preferences of bird species that occur in the mixed forests relate to the high species diversity? How are these diverse bird communities organized? What effects do modern forestry practices have on the diversity of bird communities in mixed forests? What types of management practices promote high bird species diversity in mixed forests?

DESCRIPTION OF MIXED HARDWOOD-CONIFEROUS FOREST VEGETATION

The following description of the hardwood-coniferous forests of the north central and northeastern U.S. begins by considering the presettlement forest biome. This historical approach seems worthwhile because much of the research on the dynamics of both forest and bird communities has been conducted using historical records or studying virgin relics and unmanaged forests. The same biological and physical processes illustrated in these studies continue to shape the composition of our modern, mixed forest biome, albeit altered by man's actions. A prerequisite to the management of this modern forest biome for non-game birds is an understanding of the complete range of forest environments in which the bird community evolved, and this comes only from an historical perspective.

Distribution and Composition of Forest Types

The mixed forest biome of the north-central and northeastern United States is roughly synonymous with the hemlock-white pine-northern hardwood region of Braun (1950). It covers the northern Great Lakes region, southern Quebec, Nova Scotia, New Brunswick and New England, dipping south along the Appalachian Mountains (Fig. 1). At the western boundary in northern Minnesota the biome grades into parkland and prairie; to the north, it is replaced by

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Table 1.--Comparisons of bird species diversity in various forest communities in the northeastern and north central United States[1]

Community Type[2]	Forest composition	Average No. of bird species per census route	Average species diversity index[3] per census route
Spruce-Hardwood	mixed	60.3	3.377
Adirondack Mountain	mixed	61.3	3.457
Northern Hardwoods	mixed	63.3	3.508
Wisconsin Driftless Area	deciduous	58.1	3.123
Eastern Lake Section	deciduous	54.4	2.938
St. Lawrence Valley	deciduous	55.9	3.063
Allegany Plateau	deciduous	54.9	3.135
Closed Boreal Forest	coniferous	51.5	3.262

[1] Data from an analysis of Breeding Bird Surveys (1968-1973) by Peterson (1975).

[2] See map in Peterson (1975).

[3] Calculations based on Shannon-Weaver function (Tramer 1969).

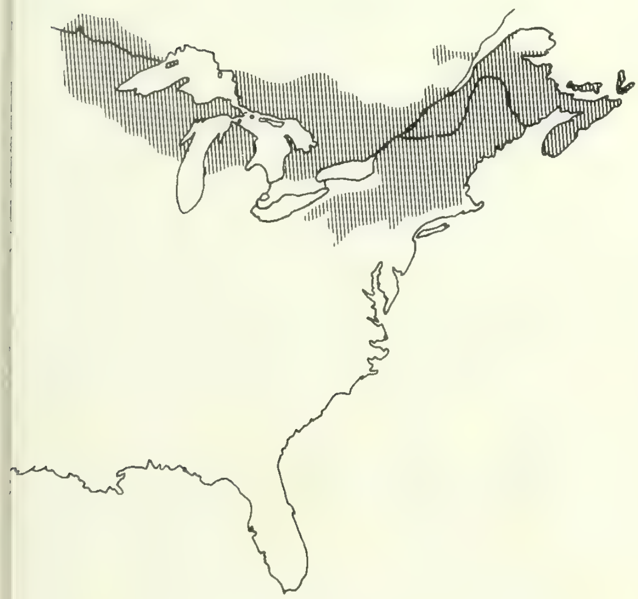

Figure 1.--The geographic distribution of mixed hardwood-coniferous forests in the north central and northeastern United States (adapted from Braun's (1950) map of the hemlock-white pine-northern hardwoods region). Forests within this region differ in their species composition, but all are mixed forests.

boreal forest and to the south by southern deciduous forest, savanna and mixed forest of the southern Appalachians. Various associations of hardwood-coniferous forest occur throughout this biome.

Curtis (1959) has given a most complete regional description of the presettlement hardwood-coniferous forest community. The major dominant tree species of the upland mixed forests of Wisconsin are, in order of increasing shade tolerance: jack pine, (*Pinus banksiana*); hill's oak, (*Quercus elipsoidales*); quaking aspen, (*Populus tremuloides*); red pine, (*P. resinosa*), white pine, (*P. strobus*); paper birch, (*Betula papyrifera*); red oak, (*Q. borealis*); red maple, (*Acer rubrum*); yellow birch, (*B. lutea*); basswood, (*Tilia americana*); hemlock (*Tsuga canadensis*); beech, (*Fagus grandifolia*); and sugar maple, (*A. saccharum*). Table 2 summarizes the composition and structure of typical stands of mixed forest in Wisconsin.

There are several geographic trends in the biome. In the extreme western portion of the biome, beech, hemlock and yellow birch successively disappear and white pine and basswood increase in importance. East of Wisconsin, red spruce (*Picea rubens*), sweet birch (*Betula lenta*) and gray birch (*B. populifolia*) join the forest and increase in importance along with hemlock and beech; jack pine, red pine and yellow birch decline. These compositional changes often involve the replacement of one species by an ecological equivalent with a similar life-form so that the physiognomy of the

Table 2.--Structure and composition of typical stands of hardwood-coniferous forest.[1/]

Locality and Species	Plants per acre Less than 1" d.b.h.		Plants per acre More than 1" d.b.h.				
	Less than 1"tall	More than 1"tall	1-4"	4-10"	10-20"	20-30"	30+"
a. Wet-mesic swamp of cedar and fir in Vilas County, Wisconsin							
Abies balsamea	3800	1000	56	200	0	0	0
Acer rubrum	3000	200	39	9	4	0	0
Betula lutea	1600	0	0	0	7	0	0
B. papyrifera	0	0	3	44	14	0	0
Fraxinus nigra	400	400	0	19	0	0	0
Picea mariana	0	0	0	3	0	0	0
Populus tremuloides	0	0	0	0	4	0	0
Sorbus americana	1000	0	9	6	0	0	0
Thuja occidentalis	10,400	0	76	31	14	0	0
Quercus borealis	400	0	0	0	0	0	0
b. Mesic forest in Vilas County, Wisconsin							
Abies balsamea	40	15	23	1	0	0	0
Acer saccharum	20,160	5680	72	36	16	2	0
Betula lutea	7100	7	6	3	20	3	0
Ostrya virginiana	80	100	18	6	0	0	0
Picea glauca	0	0	0	0	0	1	0
Pinus strobus	0	0	0	0	2	2	1
Tilia americana	130	65	15	6	7	0	0
Tsuga canadensis	260	2	17	18	18	4	0
Ulmus americana	65	90	5	8	4	3	0
c. Mesic forest in Door County, Wisconsin							
Acer saccharum	17,280	960	11	17	41	0	0
Betula papyrifera	0	0	1	12	0	0	0
Fagus grandifolia	0	0	1	12	0	0	0
Fraxinus americana	2560	480	0	0	0	0	0
Ostrya virginiana	640	1440	3	0	0	0	0
Pinus strobus	0	0	0	0	2	1	1
Prunus serotina	160	0	0	1	0	0	0
Quercus borealis	160	0	0	0	2	0	0
Tsuga canadensis	0	0	6	0	4	1	0
d. Dry-mesic red pine forest in Oneida County, Wisconsin							
Acer rubrum	3400	1000	80	25	0	0	0
Betula papyrifera	0	0	35	31	2	0	0
Pinus resinosa	0	0	5	7	67	0	0
P. strobus	2800	1400	27	5	3	4	0
Populus grandidentata	0	0	3	5	1	0	0
P. tremuloides	0	0	1	3	1	0	0
Quercus borealis	400	0	23	24	1	0	0
e. Dry jack pine forest in Burnett County, Wisconsin							
Acer rubrum	312	62	14	6	2	0	0
Betula papyrifera	0	0	0	9	0	0	0
Pinus banksiana	0	144	71	59	33	0	0
P. strobus	164	20	0	0	2	0	0
Populus tremuloides	0	0	0	7	0	0	0
Quercus ellipsoidalis	1568	865	68	43	11	0	0

[1/] After Curtis (1959).

forest, which is so important to the bird community, changes less than a list of tree species might indicate.

Topography also varies from west to east as the gentle, glacial landscape of the lake states gives way to the montane landscape of Pennsylvania, New York and New England. In the lake states, variation in forest composition is often associated with changes in the underlying glacial deposits and in the depth of the water table which varies with slight changes in topography. The eastern region was also glaciated, but montane topography has a dominant influence upon the vegetation which varies with changes in altitude, exposure and bedrock(Braun 1950).

Within the mixed hardwood-coniferous forest, boreal elements such as black and white spruce (*Picea mariana* and *P. glauca*) increase toward the north while deciduous species such as the maples and oaks increase towards the south. In a sense, the biome may be considered a broad zone of transition or an ecotone between the boreal forest and southern deciduous forests; however, it is largely composed of unique tree and shrub communities which include important tree species that are essentially limited to the mixed forest biome (Braun 1950).

The composition of the upland, mixed forest on any particular site is determined by a complex interplay of edaphic factors, climate, succession, gap phase (sensu Watt 1947) disturbances (such as windthrows, disease and insect damage), and catastrophic disturbances (such as blowdowns, fire and insect or disease epidemics). The interaction of these biotic and physical factors constantly alters the forest environment, shifting the competitive advantage in a given locale from one tree species to another and creating a mosaic of forest types.

In the absence of disturbance, the replacement of shade intolerant trees by tolerant species and changes in the soil would theoretically result in a homogeneous climax forest over much of the hardwood-coniferous forest biome. Throughout much of the lake states region, sugar maple would become the single dominant tree. Largely because of disturbance, the mixed forest has never been dominated by one or a few shade tolerant species. Relatively small gaps in the canopy create favorable conditions for the growth of yellow birch, basswood, elms (*Ulmus americana; U. rubra*), white ash (*Fraxinus americana*), red maple and, if the gap is sufficiently large, white pine. Windthrown trees provide ideal seed beds for hemlock which is shade tolerant once established as a seedling. Catastrophic events often create conditions favorable for shade-intolerant pioneer species such as the pines, quaking aspen, paper birch and pin cherry (*Prunus pensylvanica*). However, catastrophic disturbances, when not associated with fire, and small scale disturbances of mesic forest do not necessarily lead to the establishment and growth of pioneer or gap phase species, but may be followed instead by the immediate reestablishment of mesic species from sprouts, and existing seedlings and saplings. This interplay of succession and disturbance tends to favor mixed forests over homogeneous forests of coniferous or hardwood species. Studies throughout the hardwood biome indicate that the dominant, presettlement forests were mixed hardwood-coniferous forests at various successional stages (Lutz 1930; Bromley 1935: Nichols 1935; Hough 1936; Graham 1941; Curtis 1959; Marsh 1965; Carroll 1973).

Successional Patterns in Mixed Hardwood-Coniferous Forests

Figure 2 outlines the basic pathways that succession follows, the effects of disturbances, and the relationship of mixed hardwood-coniferous forests to the other forest communities of the north central and northeastern regions. Table 2 shows the tree composition of typical stands of mixed forest. The structure and composition of stands is determined by a complex of environmental factors that results in variations in composition that follow major environmental gradients.

Rather than disrupting the mixed forest biome, fire, windthrow and other disturbances have contributed to a rich plant community by maintaining a dynamic balance between tree species (Graham 1941; Stearns 1949; Loucks 1970). In the presettlement hardwood-coniferous forests, this interplay of succession and disturbance created a complex mosaic of forest types in which all successional stages of forest were represented by stands of varying age and species composition (Watt 1947; Braun 1950; Bray 1956; Curtis 1959; Carroll 1973). This complex physiognomy has been an important factor in the evolution and persistence of the diverse community of birds in the biome. The diverse life-forms, vertical patterns of vegetation, and successional types present in the hardwood-coniferous forest provide a rich variety of habitats and resources for birds, allowing many species to coexist. Furthermore, localized changes in the composition of the forest vegetation through succession and disturbance continually alter the competitive environment for

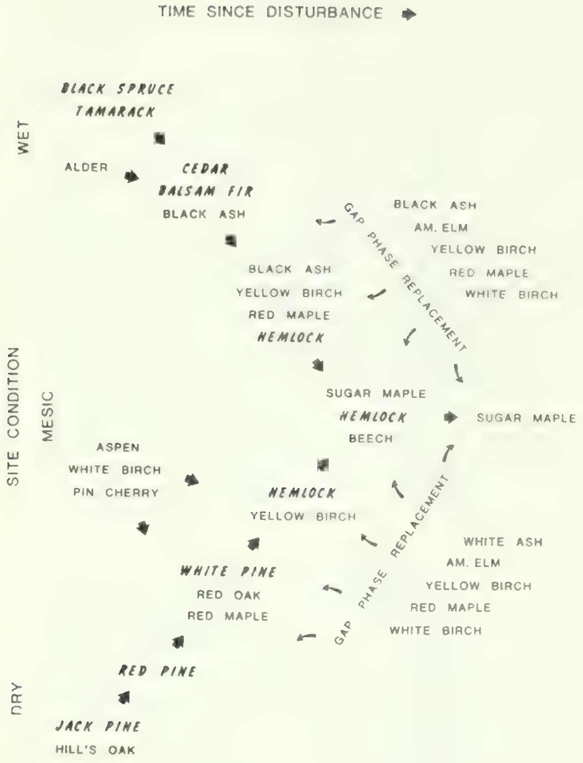

Figure 2.-- A generalized scheme of forest succession in the mixed hardwood-coniferous forests of northern Wisconsin. Succession follows the arrows from left to right. Coniferous trees are italicized.

the resident birds species, preventing a single species or group of species from dominating the entire forest bird community.

Alterations of the Mixed Forests in Historical Times

Beginning with European settlement, historical changes have altered the species composition and physiognomy of the hardwood-coniferous forests. Some of these changes are permanent. Although local economic conditions, technology and the motivation of the early settlers and those who followed varied from New England to the Midwest, the various accounts of settlement reveal a common chronology of change throughout the biome.

Beginning with the arrival of the first settlers, selective cutting of the most economically valuable trees eliminated white pine from large tracts of mixed forest (Marsh 1965; Carroll 1973). In Wisconsin, pine was removed from forests where it grew at a density of only 3 or 4 trees per acre (Curtis, 1959). Following this high grading, the forest was clear-cut for timber and/or to clear the land for agriculture. Clear-cutting increased soil erosion, disrupted the water cycle and dried out the remaining forests (Marsh 1973; Curtis 1959). Fueled by slash, the incidence of forest fires and intense crown fires increased, further limiting the distribution and reproductive potential of those species sensitive to fire, such as hemlock and white pine (Curtis 1959).

Land in many areas proved uneconomical for farming and was abandoned (Curtis 1959; Marsh 1973). This land succeeded to second growth forest of shade intolerant trees or was reforested with selected species. In areas where agricultural land-use continued, the forest persisted as isolated woodlots in a rural landscape (Curtis 1956). Chestnut blight and dutch elm disease virtually eliminated the chestnut (*Castanea dentata*) and American elm from the biome, and increased populations of herbivores such as white-tailed deer and porcupine also had some impact, especially on hemlock, white cedar and white pine.

These historical changes reduced the amount of mixed hardwood-coniferous forest by eliminating hemlock and pine from many areas of deciduous forest; favored early successional species; and created a younger, less diverse, second-growth forest with a simple vertical profile.

Modern forestry practices are leading to managed succession throughout much of the biome. The two principle management strategies are even-aged management by clear-cutting or shelterwood and uneven-aged management by selective cutting. The former has most frequently been used to perpetuate shade intolerant species while the latter can only be used to manage shade tolerant species. The physiognomy of the forest which results from either management practice depends upon the length of rotation in even-aged management, the minimum merchantable size-class in uneven-aged management, and the area and configuration of timber stands. In the past, these management decisions have been made without regard to the bird communities of the biome. Whereas uneven-aged management and selective cutting could closely simulate gap phase disturbance, it is generally used to encourage the most valuable species and to eliminate poorly shaped individuals and uneconomical species (Curtis 1959). Clear-cutting and shelterwood management could also simulate disturbances such as blowdowns and fire, but have been used most frequently to favor single, homogeneous orest types on short rotations. The manageent practices continue the post-settlement attern of: maintaining a forest of simple physiognomy by favoring conifer or hardwood forests over mixed forests; favoring early uccessional stages; and maintaining a young orest with a simple vertical profile.

The modern hardwood-coniferous forest is less complex and heterogeneous than the forst in which the birds of this biome evolved. In light of our current understanding of the effect that the spatial complexity of an environment has upon the distribution of birds pecies and the density and diversity of the bird communities, one would conclude that these differences have probably affected he bird community of the biome. The contrast between the presettlement and modern lant communities is a logical source of hypotheses related to the management of the biome for non-game birds.

SOURCES OF INFORMATION ON BIRD COMMUNITIES

The following discussion of bird communities of the mixed hardwood-coniferous forests is based on a combination of our own field work in the mixed forests of Wisconsin from 1976 to present and on the published accounts of other researchers. In Wisconsin, we have studied the bird communities of mixed forests primarily in two localities: the Apostle Islands in Lake Superior and the Baraboo Hills in central Wisconsin. The vegetation and general ecology of the Apostle Islands have been described by Beals and Cottam (1960) and the vegetation of the hardwood-coniferous forests in northern Wisconsin has been described by Brown and Curtis (1952). Lange (1976) describes the vegetation of the Baraboo Hills, a unique region slightly south of the normal range of mixed forests, which because of its topography supports typical hardwood-coniferous forest types. Less intensive field work has taken place in several other localities in northern Wisconsin, such as the Chequamegon National Forest and the Red Cliff Indian Reservation.

Within these study areas we have used a variety of techniques to study bird communities. We used the census procedures developed by Emlen (1971, 1977) to determine the species composition of the bird communities and the population densities of each species. We described the habitats occupied by breeding birds using the procedures described by James (1971) and James and Shugart (1970). In the Baraboo Hills we also used IPA mapping procedures (Ferry and Frochot 1970) to determine population densities.

BIRD COMMUNITIES OF HARDWOOD-CONIFEROUS FORESTS

Species Diversity

The high bird species diversity of the mixed hardwood-coniferous forests is one of the most important community characteristics that needs to be understood. Table 1 shows that the diversity of mixed forests exceeds the diversity of both the boreal coniferous forests, which are located to the north, and the deciduous forests to the south. There are two possible explanations for the biome's elevated species diversity. One possibility is that there are a large number of bird species restricted in geographic distribution to the mixed forests. Together these mixed-forest specialists might elevate the species diversity above that found to the north or south of the biome. Udvardy (1963) analyzed the distribution patterns of forest birds in North America. He found that mixed hardwood-coniferous forests contained only 5 species that had both the centers of their ranges and the majority of their ranges located in areas of mixed forest: the nashville warbler, black-throated blue warbler, blackburnian warbler, chestnut-sided warbler, and canada warbler. The overlap of these species' ranges with the distribution of mixed forests is not precise, and even within the mixed hardwood-coniferous forest biome, the specific habitat perferences of these species do not suggest that they are mixed forest specialists. Therefore, it does not seem likely that the high bird species diversity is the result of species being restricted to the mixed forests.

An alternative explanation is that there are a large number of bird species whose ranges lie primarily to the north or south of the mixed forests but overlap in the intervening areas. Thus, the bird communities of the hardwood-coniferous forests contain a mixture of bird species that are most typical of forest types to the north or south. In this respect, the avifauna of the mixed forests would be reacting to the mixed forests as an ecotone. It is well known that species diversity is often elevated in ecotones; this occurs apparently because species from each of the two adjoining biomes find suitable areas or patches of habitat, thus permitting coexistence within the ecotone and enriching its species diversity. Apparently this type of species enrichment occurs in the mixed forests; boreal forest and deciduous forest birds occur together in the mixed forests. Table 3 shows the north-south extent of the ranges of various mixed forest birds within Wisconsin, a state which has deciduous forests in its southern tier, mixed forests over the central regions, and coniferous forest in the far north. It is clear that the avifauna of these mixed forests is comprised of species that have extended their

Table 3.--Distributions of breeding forest birds of Wisconsin with respect to the distributions of deciduous, mixed hardwood-coniferous, and boreal coniferous forests[1/]

(Extent of Species' Range)

S. Wisconsin ←——————————————→ N. Wisconsin

Breeding bird species	Deciduous forest	Mixed forest	Boreal forest
Sharp-shinned Hawk		XXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Cooper's Hawk	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Goshawk		XXXXXXXXXX	XXXXXXXXXX
Red-shouldered Hawk	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Broad-winged Hawk	XXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Spruce Grouse		XXXX	XXXXXXXXXX
Ruffed Grouse	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Mourning Dove	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Yellow-billed Cuckoo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Black-billed Cuckoo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Long-eared owl		XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Great Gray Owl		XXX	XXXXXXXXXX
Barred Owl	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Great Horned Owl	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Ruby-throated Hummingbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Red-headed woodpecker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Red-bellied Woodpecker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXX	
Flicker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Pileated Woodpecker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Downy Woodpecker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Hairy Woodpecker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Yellow-bellied Sapsucker	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Northern 3-toed Woodpecker		XXX	XXXXXXXXXX
Black-backed Woodpecker		XXXXXXXXXXXXXX	XXXXXXXXXX
Crested Flycatcher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Olive-sided Flycatcher		XXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Least Flycatcher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Alder Flycatcher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Acadian Flycatcher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXX	
Yellow-bellied Flycatcher		XXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Eastern Phoebe	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Wood Pewee	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Gray Jay		XXXXXXXXXX	XXXXXXXXXX
Blue Jay	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Crow	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Raven		XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Tufted Titmouse	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXX	
Black-capped Chickadee	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Boreal Chickadee		XXXXXXXXXX	XXXXXXXXXX
Brown Creeper		XXXXXXX	XXXXXXXXXX
White-breasted Nuthatch	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Red-breasted Nuthatch		XXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Bewick's Wren	XXXXXXXXXXXXXXXXXXXXXX		
House Wren	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Winter Wren		XXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Carolina Wren	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXX	
Brown Thrasher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Mockingbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXX	
Gray Catbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
American Robin	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Eastern Bluebird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Olive-backed Thrush		XXXXXXXXXXXXXX	XXXXXXXXXX
Gray-cheeked Thrush		XXX	XXXXXXXXXX
Wood Thrush	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Hermit Thrush		XXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX

ble 3.--Continued

eeding bird species	(Extent of Species' Range) S. Wisconsin ← Deciduous forest	Mixed forest	→ N. Wisconsin Boreal forest
ery	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
by-crowned Kinglet		XXXXXXXXXXXX	XXXXXXXXXX
lden-crowned Kinglet		XXXXXXXXXXXXXXXXX	XXXXXXXXXX
ue-gray Gnatcatcher	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXX	
dar Waxwing	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ll's Vireo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXX	
d-eyed Vireo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
rbling Vireo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
llow-throated Vireo	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXX	
litary Vireo		XXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ack-and-White Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
othonotary Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXX	
lden-winged Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ue-winged Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXX	
shville Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
rula Warbler		XXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
llow Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
gnolia Warbler		XXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
lack-throated Blue Warbler		XXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
llow-rumped Warbler		XXXXXXXXXXXXXXX	XXXXXXXXXX
lack-throated Green Warbler		XXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
erulean Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXX	
lackburnian Warbler		XXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
hestnut-sided Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ine Warbler	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXX	
alm Warbler		XXXXXXXXXXX	XXXXXXXXXX
venbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
orthern Waterthrush	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ouisiana Waterthrush	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXX	
onnecticut Warbler		XXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ourning Warbler	XXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ommon Yellowthroat	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ellow-breasted Chat	XXXXXXXXXXXXXXXXXXXXXXXX	XXXX	
anada Warbler	XXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
merican Redstart	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
rchard Oriole	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXX	
orthern Oriole	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
rown-headed Cowbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
rewer's Blackbird	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ommon Grackle	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
carlet Tanager	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ardinal	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
ose-breasted Grosbeak	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Purple Finch		XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Pine Siskin		XXXX	XXXXXXXXXX
Red Crossbill		XXXXXXXXXXXXXXXX	XXXXXXXXXX
White-winged Crossbill		XXXXXXXXXXXXXXXX	XXXXXXXXXX
Rufous-sided Towhee	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Dark-eyed Junco		XXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
White-throated Sparrow	XXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX
Fox Sparrow		XXXXX	XXXXXXXXXX
Song Sparrow	XXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXXX	XXXXXXXXXX

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[1] Distributions of forest types taken from Curtis (1959); distributions of birds taken from Gromme (1963).

ranges into mixed forest from the north or south.

The key to the maintenance of this high bird species diversity is the spatial complexity of the forest. Both the vertical and horizontal complexity of the vegetation are known to affect bird species diversity (MacArthur and MacArthur 1961), and it seems likely that horizontal complexity is relatively more important than vertical complexity in promoting diversity in the mixed forests. As we mentioned in our discussion of the physiognomy of the forest, one important characteristic of the forest is its patchiness. Hardwoods and conifers rarely form a truely homogeneous mixture. Rather, the dispersion of tree-types is contagious or clumped: both coniferous and deciduous trees tend to be found in discrete patches or groves. This dispersion pattern allows birds that are primarily adapted for coniferous vegetation to select patches of conifers in which to establish breeding territories, whereas those birds that are primarily adapted for living on deciduous vegetation can select patches containing predominantly deciduous trees in which to establish territories.

To demonstrate this selection by birds of patches of vegetation that are either more northerly or southernly in their affinities, we analyzed the vegetation within the territories of several warbler species breeding in the mixed forests of the Baraboo Hills of Wisconsin. Figure 3 shows the strong correlation between the northern affinity of the vegetation within a bird's territory and the percentage of that particular species range (on a north-south basis) that lies to the north of the site. Clearly, the bird species that have the most northerly geographic distributions are selecting for their territories those patches of forest that include the most northerly types of vegetation. The converse is true for southern bird species.

It seems that most birds of the mixed forests are not responding to the mixed forests as a single type of vegetation. Rather they are responding to the mixed forest as a mosaic of vegetation patches with either northerly or southerly affinities. This may be one of the most important ecological characteristics of the birds that breed in mixed forests, and as we shall mention later, it is perhaps the most important characteristic with relevance to forest management.

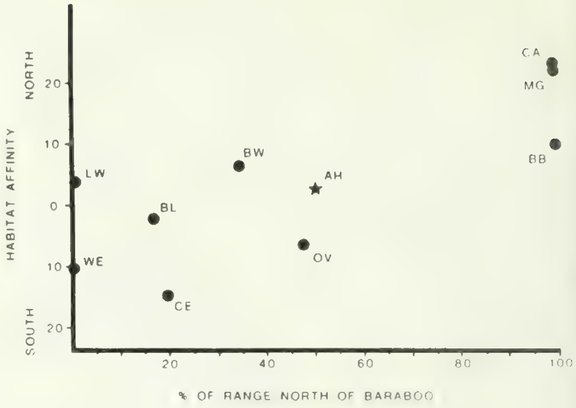

Figure 3.--The relationship between the geographic distribution of a species and the type of vegetation within its territory in the Baraboo Hills of central Wisconsin. The percent of range north of Baraboo was measured along the 90th meridean. Habitat affinity was calculated as N-S/N+S, where N is habitat similarity with Curtis' (1959) northern Wisconsin forest types and S is the similarity with southern Wisconsin forest types. Similarities were calculated as "coefficients of community" (Gleason 1920) using importance values for tree species. LW=Louisiana Waterthrush, WE=Worm-eating Warbler, BL=Blue-winged Warbler, CE=Cerulean Warbler, BW=Black-and-White Warbler, OV=Ovenbird, BB=Blackburnian Warbler, MG=Magnolia Warbler, CA=Canada Warbler, AH=available habitat.

Bird Population Densities In Hardwood-Coniferous Forests

Although mixed hardwood-coniferous forests are somewhat unique for their high bird species diversities, they are not very unusual in terms of the densities of birds that they support. From our own work and published accounts, we have assembled some representative breeding bird population densities for various types of mixed forest in the north central and northeastern U.S. (Table 4). These data suggest that most mixed-forest stands can be expected to support bird densities on the order of 150-300 territorial birds per 100 acres (40ha) during the breeding season. These figures are not very different from bird population densities reported for either boreal coniferous forests or northern hardwood forests.

Bird population densities are known to be affected by the productivity of the habitat that the birds are occupying. It seems reasonable, therefore, to expect that some, if not most, of the inter-stand variability in bird population densities in mixed forests can be accounted for by differences in productivity. In particular, for the majority of forest birds, which are primarily insectivorous able 4.--Population densities of breeding birds in various stands of mixed hardwood-coniferous forest in north central or northeastern United States.

Species	Sources of Data[1/] 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A. Percent composition of vegetation in study area[2/]																
White cedar	+	0		0	0		+	0	0	0		0	0		0	
Hemlock		4		0	0		+	0	0	20	+	20	6	+	74	+
Pine		69		0	0		0	0	20	60	+	7	0		0	
Spruce-fir		0	+	73	90	++	34	53	0	0		0	0		0	
Total coniferous		73		73	90		41	53	20	80		27	6		74	
Maple-beech				0	1		+	24	20		++	20	56	++	23	
Yellow birch				0	9		+	23	7		+	10				
Aspen-white birch	+	22	+	27	0		0	0	5			0				
Total deciduous		27		27	10	+	59	47	80	20		73	94		26	
B. Bird population densities (pairs/40ha)[3/]																
Mourning dove	3	+	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Yellow-billed Cuckoo	0	0	0	0	0	0	0	0	0	0	0	+	0	+	0	0
Black-billed Cuckoo	0	0	0	0	0	0	0	0	0	0	1	0	0	+	0	0
Turkey Vulture	0	0	0	0	0	0	0	0	+	0	0	+	0	0	0	0
Goshawk	0	0	0	0	0	0	0	0	+	0	0	0	0	0	0	0
Coopers Hawk	0	0	0	0	0	0	0	0	+	0	+	0	0	0	0	0
Sharp-shinned Hawk	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Red-tailed Hawk	0	0	0	0	0	0	0	0	+	0	0	+	0	0	0	0
Red-shouldered Hawk	0	0	0	0	+	0	0	+	+	0	0	+	0	0	0	0
Broad-winged Hawk	0	0	0	0	0	0	0	0	0	0	+	0	0	0	0	1
Peregrine Falcon	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Merlin	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Ruffed Grouse	0	1	0	0	0	6	0	+	+	1	+	+	3	+	2	0
Great-horned Owl	0	0	0	0	0	0	0	0	0	+	0	0	+	0	+	0
Long-eared Owl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barred Owl	0	0	0	0	0	0	0	0	2	0	1	2	0	1	0	1
Saw-whet Owl	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common Nighthawk	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Whip-poor-will	0	0	0	0	0	0	0	0	0	1	0	+	0	0	0	0
Chimney Swift	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ruby-throated Hummingbird	+	0	3	0	0	0	0	0	1	0	+	4	0	0	0	0
Common Flicker	3	2	0	+	0	0	0	0	3	0	0	+	0	+	0	2
Pileated Woodpecker	0	0	0	+	0	0	0	+	2	+	+	+	+	+	+	1
Red-bellied Woodpecker	0	0	0	0	0	0	0	0	4	0	0	+	0	1	0	0
Red-headed Woodpecker	0	0	0	0	0	0	0	0	1	0	0	+	0	0	0	0
Yellow-bellied Sapsucker	3	0	6	0	0	3	3	0	0	2	0	0	0	0	0	0
Hairy Woodpecker	3	1	0	0	+	+	1	3	2	3	1	4	2	4	3	3
Downy Woodpecker	1	+	0	0	0	0	0	0	6	2	0	2	0	5	0	2
Eastern Kingbird	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Great-crested Flycatcher	3	2	0	0	0	0	0	0	6	1	1	+	3	3	1	0
Eastern Phoebe	0	0	0	0	0	0	0	0	3	0	0	6	0	2	0	0
Yellow-bellied Flycatcher	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0
Acadian Flycatcher	0	0	0	0	0	0	0	0	8	0	0	36	0	5	0	0
Least Flycatcher	0	0	0	4	0	0	0	0	0	0	6	36	0	0	0	0
Eastern Pewee	3	16	0	0	0	0	6	0	14	6	14	16	1	10	0	0
Olive-sided Flycatcher	0	0	0	+	0	0	0	0	0	2	0	0	0	0	0	0
Tree Swallow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bluejay	3	2	3	0	+	+	3	3	11	2	1	4	2	1	2	0

Table 4.--Continued.

Species	Sources of Data[1]															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Gray Jay	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	+
Common Raven	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Common Crow	0	+	0	+	0	0	0	0	+	0	1	0	0	0	0	0
Black-Capped Chickadee	5	8	6	2	4	6	9	2	6	6	3	8	3	5	9	14
Carolina Chickadee	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0
Boreal Chickadee	0	0	0	5	0	0	+	0	0	0	0	0	0	0	0	0
Tufted Titmouse	0	0	0	0	0	0	0	0	0	0	0	+	0	9	0	0
White-breasted Nuthatch	0	0	0	0	0	0	0	0	6	1	2	6	2	5	5	0
Red-breasted Nuthatch	1	1	0	4	13	3	0	7	0	1	0	0	0	0	0	10
Brown Creeper	0	0	0	0	0	0	0	7	0	1	0	0	0	0	0	7
House Wren	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Winter Wren	13	0	0	4	0	0	0	3	1	1	1	0	0	0	0	5
Carolina Wren	0	0	0	0	0	0	0	0	0	0	0	0	0	+	0	0
Gray Catbird	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
Brown Thrasher	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Robin	7	12	3	16	8	3	1	3	6	0	1	2	0	1	0	0
Wood Thrush	0	0	0	0	+	3	0	3	7	0	2	10	0	22	1	0
Hermit Thrush	0	8	6	+	8	0	1	3	0	10	0	0	5	0	6	5
Swainson's Thrush	0	0	0	21	4	1	14	13	0	0	0	0	0	0	0	3
Veery	0	+	9	0	+	18	0	7	8	5	8	6	4	0	5	0
Blue-gray Gnatcatcher	0	0	0	0	0	0	0	0	8	0	0	16	0	0	0	0
Golden-crowned Kinglet	0	0	7	0	33	0	0	32	0	0	1	0	0	0	0	2
Ruby-crowned Kinglet	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	+
Cedar Waxwing	0	4	0	0	0	0	0	0	1	0	1	+	0	0	0	0
Starling	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solitary Vireo	3	0	0	2	17	0	3	26	0	4	0	0	0	0	1	2
White-eyed Vireo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yellow-throated Vireo	0	0	0	0	0	0	0	0	2	0	1	6	0	3	0	0
Red-eyed Vireo	3	1	17	14	0	20	54	10	14	10	32	36	25	14	1	17
Philadelphia Vireo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Warbling Vireo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Black & White Warbler	13	0	8	+	0	17	0	0	2	8	1	0	3	0	2	5
Worm-eating Warbler	0	0	0	0	0	0	0	0	1	0	0	+	0	0	0	0
Golden-winged Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Blue-winged Warbler	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Tennessee Warbler	0	0	0	+	0	0	0	0	0	0	0	0	0	0	0	0
Nashville Warbler	10	0	6	19	0	9	0	0	0	0	0	0	0	0	0	3
Northern Parula Warbler	7	0	0	4	+	0	26	3	0	0	0	0	0	0	0	5
Yellow Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Magnolia Warbler	0	0	17	32	42	31	10	45	0	4	0	8	2	0	25	9
Cape May Warbler	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Yellow-rumped Warbler	3	+	6	26	0	6	+	0	0	2	0	0	0	0	0	17
Black-throated Green Warbler	3	16	0	0	21	6	23	31	0	13	8	0	9	4	32	28
Black-throated Blue Warbler	5	0	0	0	21	3	29	16	0	6	2	0	6	0	9	0
Cerulean Warbler	0	0	0	0	0	0	0	0	+	0	0	4	0	3	0	0
Blackburnian Warbler	0	0	8	2	67	15	30	55	4	18	6	2	6	0	14	102
Chestnut-sided Warbler	0	0	+	0	0	14	+	0	0	0	0	0	0	0	0	0
Bay-breasted Warbler	0	0	0	95	0	0	0	0	0	0	0	0	0	0	0	1
Blackpoll Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pine Warbler	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prairie Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Palm Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ovenbird	10	20	25	2	0	33	23	3	1	9	19	14	28	28	32	2
Northern Waterthrush	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0
Louisiana Waterthrush	0	0	0	0	0	0	0	0	8	0	0	6	0	4	0	0
Common Yellowthroat	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0	0

Table 4.--Continued.

Species	Sources of Data[1] 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Yellow-breasted Chat	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mourning Warbler	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Connecticut Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hooded Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	20	0	0
Wilson's Warbler	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Canada Warbler	3	0	14	0	0	23	0	16	6	7	0	8	4	0	10	0
American Redstart	0	0	+	4	0	18	3	0	0	6	37	0	0	17	0	0
Common Grackle	0	0	+	0	0	0	0	0	+	0	0	0	0	0	0	0
Brown-headed Cowbird	+	+	0	0	0	0	0	0	9	0	+	16	0	2	0	0
Northern Oriole	2	0	0	0	0	0	0	0	5	0	0	+	0	0	0	0
Scarlet Tanager	10	0	0	0	4	3	3	7	15	3	3	20	3	9	5	0
Cardinal	0	0	0	0	0	0	0	0	3	0	0	8	0	5	0	0
Rose-breasted Grosbeak	+	0	0	0	8	+	0	3	17	0	0	18	0	3	0	0
Evening Grosbeak	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Indigo Bunting	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0
Purple Finch	3	+	+	7	8	3	+	3	0	0	1	0	0	0	0	3
Pine Grosbeak	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0
Common Redpoll	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pine Siskin	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
American Goldfinch	0	0	0	0	+	0	0	0	2	0	0	6	0	0	0	0
Red Crossbill	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White-winged Crossbill	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vesper Sparrow	0	+	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rufous-sided Towhee	0	4	0	0	4	0	0	0	0	0	0	0	0	1	0	0
Dark-eyed Junco	3	4	+	9	33	0	0	21	0	10	0	0	0	0	0	13
Tree Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chipping Sparrow	0	4	0	0	0	0	0	0	1	0	0	0	0	0	0	2
Field Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White-throated Sparrow	10	0	15	14	0	8	0	0	0	8	0	0	0	0	0	9
Song Sparrow	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total	139	112	159	318	295	258	241	325	207	158	155	310	111	215	165	274

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[1] Sources of Data: Kendeigh, 1948 (1, 2, 11); Kendeigh, 1946 (13, 15); Martin, 1960 (3, 6, 16); Stewart and Aldrich, 1952 (4); Stewart and Aldrich, 1949 (5, 8); Mossman, unpubl. (9, 12); Smith, 1944 (10); Williams, 1947 (14); Cope and Hensley; 1951 (7).

[2] Tree composition is recorded, when available, as percent of total number of trees. + indicates presence, ++ dominance and 0 absence.

[3] + indicates presence, 0 absence, and numbers density of males or pairs.

during the breeding season, the abundance of forest insects can be an important factor in determining local bird population densities. It is well known for example, that bird populations show dramatic numerical responses to localized outbreaks of forest insects that temporarily increase the productivity of a stand (Buckner and Turnock 1965). Conversely, stands with low productivity of forest insects can be expected to have reduced bird population densities.

Relative Abundance of Bird Species

The internal composition of the bird communities of mixed hardwood-coniferous forests can be analyzed in terms of the relative abundances of the various species that are members of the communtiy. In Table 4, we have presented for various types of mixed forests the population densities of each bird species present. Comparision of these figures reveals that there is definitely a consistent group of species which can be considered dominant in most mixed forests. These include: the ovenbird, red-eyed vireo, black-throated green warbler, blackburnian warbler, black-throated blue warbler, veery, and white-throated sparrow. Each species is present at densities that are conspicuously higher than those of other species, and together these species usually comprise 20-40 percent of the total number of individuals in the community.

If we rank sequentially the relative abundances of the 15 most abundant bird species in each of several types of mixed forests, a general pattern emerges (Figure 4). Basically, there are very few really common species, a relatively small number of moderately abundant species, and a large number of fairly uncommon species within the mixed hardwood-coniferous forests, a pattern which is common to many, if not most, forest bird communities.

Habitat Affinities of Mixed Forest Birds

Several researchers have attempted to describe the specific habitat preferences of birds in mixed forests (Kendeigh 1946, 1948; Martin, 1960; Stewart and Aldrich, 1949, 1952). Beals (1960) used an ordination technique to reveal the vegetation characteristics to which birds are responding. We have also used ordinations but have followed the technique described by James (1971) which is based on the vegetation surrounding the singing perches used by territorial males and presumably, is a reflection of the vegetation in the bird's territory. We have interpreted our ordination results in terms of several characteristics of the vegetation within bird territories that are relevent to questions of forest management. These include: relative abundance of pines, relative abundance of hemlocks, relative abundance of spruce-fir, relative abundance of sugar maple, relative abundance of aspen, average basal area of trees, density of trees, relative density of understory. In Table 5, we have summarized some of our ordination results in terms of these vegetation characteristics.

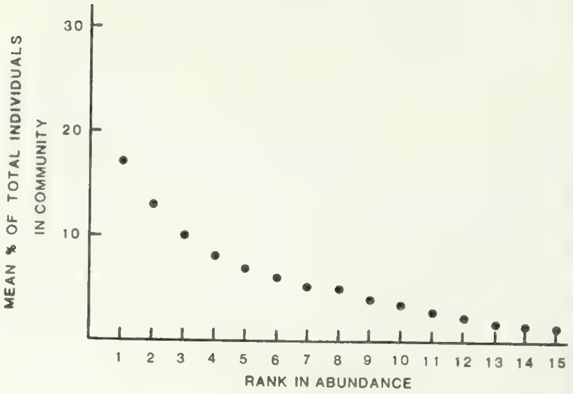

Figure 4.--The relative abundances of the fifteen most abundant bird species in various stands of mixed hardwood-coniferous forest. Data are taken from the same sources cited in Table 4.

Seasonality In Mixed Forest Bird Communities

So far we have restricted our discussion to the breeding bird communities of the mixed hardwood-coniferous forests. It is important to recognize, however, that the high bird species diversity and relatively high density of birds that characterize the mixed forests during the summer months do not prevail throughout the year. The contrast between the summer bird communities and the winter bird communities is striking. A comparison of the diversity and density of birds in two similar stands of mixed forests in northern Wisconsin, one in summer and the other in winter illustrates this. In June we detected an average of 39 species of birds per hour of censusing and an average density of 252 individuals per 100 acres (40 ha). In contrast, during our December censuses we detected an average of 5 species per hour of censusing and an average density of 16 individuals per 100 acres (40 ha).

From selected Christmas Bird Count records and our own experience, we can list the species of forest birds that regularly occur in the

Table 5.--An interpretation of habitat ordination results from breeding bird communities of mixed forests on the Apostle Islands, Wisconsin.

Alterations of vegetation within a stand	Bird species that are likely to become more abundant
1. Increasing abundance of pine	Sharp-shinned hawk, red-breasted nuthatch, hermit thrush, redstart, blackburnian warbler, Nashville warbler, pine warbler
2. Increasing abundance of hemlock	pileated woodpecker, yellow-bellied sapsucker, yellow-bellied flycatcher
3. Increasing abundance of spruce or fir	cedar waxwing, yellow-bellied flycatcher, swainson's thrush, redstart, parula warbler, blackburnian warbler
4. Increasing abundance of yellow birch and sugar maple	black-billed cuckoo, downy woodpecker, wood-pewee, least flycatcher, crow, brown creeper, veery, robin, warbling vireo, red-eyed vireo, Connecticut warbler, chestnut-sided warbler, black-throated green warbler, black and white warbler, Tennessee warbler, indigo bunting, rufous-sided towhee, rose-breasted grosbeak
5. Increasing abundance of aspen	yellow-shafted flicker, hairy woodpecker, house wren, veery, yellowthroat, mourning warbler, chestnut-sided warbler, song sparrow, white-throated sparrow
6. Increasing average basal area of trees	pileated woodpecker, solitary vireo
7. Increasing density of trees per unit area	scarlet tanager, ovenbird
8. Increasing density of understory	veery, black-throated blue warbler, Canada warbler

mixed forests of Wisconsin during winter; these include: goshawk, great horned owl, barred owl, ruffed grouse, downy woodpecker, hairy woodpecker, pileated woodpecker, bluejay, gray jay, common raven, black-capped chickadee, red-breasted nuthatch, white-breasted nuthatch, brown creeper, evening grosbeak, cardinal, and purple finch. All these species are severely limited by the restricted supply of food available in the mixed forest during the winter. Many of the species, particularly the woodpeckers, chickadees, nuthatches, and creepers, are insectivorous and forage by probing in bark or dead wood. For these species, the presence in the forest of snags, dead limbs, and old mature trees is essential.

Successional Changes in Bird Communities

Although our main concern is with the bird communities of relatively mature stands of mixed hardwood-coniferous forests, it is important to summarize briefly the changes in the composition of the bird community as a stand progresses through successional stages of vegetation. Table 6 summarizes the bird communities associated with early, middle, and late seral stages leading to a beech-maple-hemlock forest in New York State. Bird species diversity increases progressively through these successional stages whereas bird densities tend to decrease slightly. In his analysis of Breeding Bird Surveys conducted by the U.S. Fish and Wildlife Service, Peterson (1975) found that in the ecological regions dominated by mixed hardwood-coniferous forests observers detected more species of birds in total than in any other ecological region of the U.S. Within the region characterized by "Spruce-hardwood forest" observers saw an average of 194.2 species per year for the period 1968-1973. The next highest species list was recorded in the "upper coastal plain" where an average of 169.8 species was observed each year. Although the mature mixed forests support a high species diversity, many of the birds

Table 6.--Bird species associated with seral stages leading to a mature beech-maple-hemlock forest on the Helderberg Plateau of central New York state (after Kendeigh 1946).

Bird Species	Seral Stage[1/]			
	Early →	Middle →	Late →	Mature
Common Yellowthroat	+			
Song Sparrow	+			
Field Sparrow	+			
Chestnut-sided Warbler		+		
Rufous-sided Towhee		+		
Gray Catbird		+		
Alder Flycatcher		+		
Swamp Sparrow		+		
Red-winged Blackbird		+		
Indigo Bunting		+		
Brown Thrasher		+		
Yellow-breasted Chat		+		
Golden-winged Warbler		+		
American Robin			+	
American Redstart			+	
Nashville Warbler			+	
American Goldfinch			+	
Cedar Waxwing			+	
House Wren			+	
Woodcock			+	
Northern Oriole			+	
Common Flicker			+	
Eastern Kingbird			+	
Chipping Sparrow			+	
Ruby-throated Hummingbird			+	
Black-billed Cuckoo			+	
Purple Finch			+	
Mourning Dove			+	
Eastern Phoebe			+	
Eastern Bluebird			+	
Rose-breasted Grosbeak			+	
Downy Woodpecker			+	
Red-eyed Vireo			+	+
Veery			+	+
Canada Warbler			+	+
Ovenbird			+	+
Magnolia Warbler			+	+
Black-and-White Warbler			+	+
Black-capped Chickadee			+	+
Black-throated Green Warbler				+
Blackburnian Warbler				+
Black-throated Blue Warbler				+
Hermit Thrush				+
White-breasted Nuthatch				+
Scarlet Tanager				+
Hairy Woodpecker				+
Ruffed Grouse				+
Wood Thrush				+
Solitary Vireo				+
Pileated Woodpecker				+
Crested Flycatcher				+
Great Horned Owl				+
Sharp-shinned Hawk				+

[1/] Early=scattered briars, herbs, and low shrubs; middle=mature shrubs and small trees; late=scattered stands of tall trees and shrubs; mature=well-developed forest dominated by beech, maple, and hemlock.

that account for the extremely high total species list are birds of early successional stages. These early seral stages are, therefore, important in contributing to the overall bird species diversity in the regions dominated by mixed forests.

FOREST MANAGEMENT AND BIRD COMMUNITIES

We have already summarized briefly the impact that man has had on the mixed hardwood-coniferous forests of the north central and northeastern U.S. Our intent now is to outline in a general way the types of forestry practices that would promote what we feel is the single most significant ecological trait of the mixed forests bird communities: their high species diversity. First, we will list the important characteristics of the bird communities that relate to high species diversity:

(1) most forest birds respond to the mixed forest as a mosaic of patches which are either dominated by conifers or hardwoods. Few birds are actually selecting habitats that are a homogeneous blend of conifers and deciduous trees.
(2) most of the breeding birds are insectivorous and depend on a well-stratified forest with good vertical diversity in order to segregate their feeding niches.
(3) most breeding birds are insectivorous and depend on rich and varied insect populations in order to maintain high population densities.

(4) there are a few common or moderately common bird species that are dominant in the mixed forests, but the high species diversity is, in large part, the result of the many relatively uncommon species occurring in the mixed forests.
(5) from habitat ordinations, we can predict which bird species will be favored or adversely affected by specific habitat alterations.
(6) bird species diversity in mixed forests is high only during the summer; during the winter the species diversity is extremely low, and the species present have readily identifiable and fairly similar requirements of the mixed forest.
(7) maintaining a mosaic of seral stages promotes an overall diversity of birds within the regions that are dominated by mixed forests.

These ecological characteristics of the mixed forest bird communities must be reconciled with potential silviculture options in order to develop a set of management procedures that will sustain the entire complement of bird species in the biome and favor high bird species diversity.

Potential Silviculture Options For Mixed Forests

There are few specific management guidelines available for mixed forests because in almost all cases the silviculturalist is interested in either hardwoods or conifers, not a mixture of types. Tubbs (1977) provides a recent set of recommendations for the management of northern hardwoods and he includes brief descriptions of mixed stands in his discussion. Nonetheless, it seems most useful to discuss management options from the viewpoint of northern hardwood silviculture.

We will consider the following options for managing northern hardwoods: even-age management, uneven-age management and preservation. Although the effects that each of these management options would have on bird communities in mixed forests are as yet undemonstrated, we can make reasonable predictions on the basis of our knowledge of what these practices will do to the vegetation and our knowledge of what bird communities require. Although only a few specific studies of the impact of silviculture have been carried out, the recent results of Webb et al. (1977) should serve to emphasize the potential that silviculture has for altering bird communities.

Even-Aged Management

Even-aged management can be used to regenerate shade tolerant or intolerant species, and has the advantage over uneven-aged management of increased efficiency (Tubbs, 1977). Shelterwood and clear-cutting, the two methods of even-aged management most widely used, allow succession to proceed in some modified way with infrequent interventions into the forest for thinning or harvesting. Clear-cutting is generally used where the ultimate goal is reproduction of intolerant trees for pulpwood on a 50-70 year rotation, while the ultimate goal of shelterwood management is the reproduction of more valuable, shade tolerant hardwoods on a cycle of 100-120 years (Tubbs 1977).

We can identify some of the general effects that even-aged management has on mixed forest vegetation, and from these infer how bird communities are likely to respond. Shelterwood management encourages horizontal diversity of vegetation within a stand and will tend to favor a patchy distribution of tree species. This is particularly true if intermediate cuts favor moderately intolerant, as well as tolerant species, and a patchy distribution of conifers and hardwoods. Clear-cutting for pulpwood generally favors monotypic stands with a low horizontal diversity of vegetation, and the prescribed rotations of 50-70 years do not allow much diversity to develop due to natural disturbances. Both methods of even-aged management reduce the vertical diversity of vegetation within a stand by favoring single age-classes of trees, reducing the diversity of tree species, and opening the canopy. The opening of the canopy, in turn, tends to increase the development of the understory. Traditionally, the intermediate cuts reduce the density of dead and diseased trees.

In terms of the important ecological characteristics of the mixed forest bird communities, we can say that even-aged management has the following benefits and disadvantages for promoting high bird speices diversity.

(1) by promoting horizontal diversity in the forest vegetation shelterwood management can enhance bird species diversity, particularly if intermediate cuts can be made in such a way as to encourage a patchy distributuion of tree species.
(2) by reducing vertical diversity in the forest vegetation, even-aged management will tend to reduce the foraging opportunities available to birds and, hence, will reduce both the diversity and density of birds within specific patches of vegetation.
(3) by reducing the density of dead or diseased trees within a stand, even-aged management can reduce the productivity of insects in the forest and the availability of nesting cavities. This has a particularly important impact on the winter bird community which includes mostly bird species which probe in bark or wood to extract insects.
(4) from our understanding of the habitat requirements of individual bird species, we can predict some of the specific effect of even-aged management. Clear-cutting will create early seral stages and favor the bird species that prefer this type of habitat. Even-aged management will probably favor the more common members of the bird community, but may eliminate some of the less common species that contribute to high diversity.

Within the accepted guidelines for even-aged management of mixed forests there are several possibilities for minor modifications that would be beneficial to the mixed forest bird communities. We offer these as suggestions, but it should be realized that these are mostly unproven techniques:

(1) after clear-cutting or a shelterwood cut, an area is usually allowed to regenerate naturally through successional stages. The planting of small (3 ha) patches of conifers, particularly hemlocks and red or white pines, within the stand soon after cutting sould insure that conifer patches will develop. This would increase the horizontal diversity of vegetation in the stand, and would also increase vertical diversity of vegetation since conifers have a different vertical profile than hardwoods.
(2) when intermediate cuts are made to improve the quality of harvestable trees, several other objectives could simultaneously be achieved. These include allowing patches of conifers to persist within the hardwoods, preserving all snags or diseased trees that are not directly threatening valuable species, and creating snags by girdling species that are to be eliminated anyway and leaving them standing.
(3) within the constraints of silvicultural practices and economics, rotations should be as long as possible in clear-cut management, and cutting cycles should be as long as possible in shelterwood management.

Uneven-Aged Management

Uneven-aged management results in a different set of modifications of the mixed forest vegetation. Although current trends lean towards even-aged management, most of the management that has taken place in the past in mixed forests has been uneven-aged silviculture (Tubbs. 1977).

Under an uneven-aged management program, individual trees within the stand are selected for harvest or culling on the basis of species, age, diameter, and form. Maximum tree size in a stand depends upon whether management is for pole lumber or saw logs. The periodic removal of highly desirable trees from the forest results in several changes in forest vegetation that can have an impact upon bird communities. Uneven-aged management favors shade tolerant species which can reproduce under the canopy. The development of shade tolerant seedlings and saplings along with the growth of shrubs in canopy openings created by selective cuts, creates a forest which is vertically diverse. This vertical diversity is enhanced where the maximum tree size is large, and is reduced where it is small. The elimination of intolerant trees reduces the horizontal diversity of the forest. As in uneven-aged management, diseased, poorly formed and uneconomical trees are culled. Conifers cannot be maintained in a stand by uneven-aged management.

We can make some predictions about the impact that uneven-aged management would have on bird communities in the mixed hardwood-coniferous forests, but again there has been almost no research that would clearly prove these predictions valid. The following, however, seem to be the likely outcomes:

(1) by enhancing vertical diversity in the forest vegetation, uneven-aged management will favor high densities of a few species of birds.
(2) by reducing horizontal diversity, uneven-aged management will tend to depress the overall species diversity within the stand.
(3) by reducing the density of snags and overmature trees, uneven-aged management reduces the availability of insects for certain birds, particularly those that overwinter in the forest.
(4) by maintaining the forest in a seral stage close to the climax, uneven-aged management reduces the overall bird species diversity of a region by eliminating the early seral-stage habitats that some birds require. However, this may provide habitat for bird species of the forest interior which may not find suitable habitat in younger stands.
(5) when compared with even-aged management, uneven-aged management results in more frequent disturbance of the forest for harvesting, but the disturbance is not as severe as in even-aged management. Various bird species may respond in different ways to the frequency and severity of disturbance.

We can again offer some unproven suggestions for modifying current uneven-age management procedures in such a way that bird communities will benefit; these include:

(1) increasing horizontal diversity within a stand by either planting small patches (about 3ha) of conifers or allowing patches of conifers to develop and persist.
(2) simulating gap phase replacement by periodically opening up small patches and allowing them to pass through normal succession
(3) allowing snags to persist, as was suggested under even-aged management.
(4) cutting trees only of the largest size class that is economically feasible, thus maximizing vertical diversity of the stand.

Preservation

Preservation as a management practice is less well defined than the two options previously discussed. It may range from a completely "hands-off" policy, to active management for maximum esthetic and recreational benefits. For this discussion we take preservation to mean minimal intervention with management for esthetics, scientific research and/or wilderness recreation. If enough land were managed by preservation (i.e., thousands of hectares), this would result in mixed forest vegetation similar to the presettlement forests in which succession and disturbance created a mosaic of vegetation types with high horizontal and vertical diversity. On smaller management units the results of preservaiton will be less predictable. Small areas are likely to be maintained as a single seral stage by succession or catastrophic disturbances, such as ice and wind storms or fire.

Management by preservation has the following benefits and disadvantages for promoting high bird species diversity:

(1) tracts of land which are sufficiently large can offer horizontal and vertical diversity of vegetation that supports a diverse avian community.
(2) smaller areas of land will have a more uniform vegetation type which may be suddenly changed by catastrophic disturbances. Their contribution to an area's bird diversity will depend entirely upon whether they supply a unique habitat.

Recommendations for managing these areas for birds follow directly from these and include:

(1) large tracts of wildlands should be managed so as to allow natural succession and disturbance to occur and, thus, create diverse habitats for birds.

(2) if managing for the diversity of bird species is the principle goal, it is inappropriate to manage small areas of mixed forest by preservation. If small tracts of land are not to be economically exploited, they would best be managed for a forest type which is unavailable in the area.

Our management recommendations are specifically aimed at increasing the vertical and horizontal diversity of forests which are managed for lumber, pulpwood and other uses, thereby simulating the mosaic pattern of vegetation characteristic of the primeval forest. As we currently understand the dynamics of bird communities, this strategy will help sustain the full complement of the bird species of the hardwood-coniferous forest and maintain the region's high species diveristy.

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APPENDIX I

Common and scientific names of bird species mentioned in the text

Turkey Vulture (*Cathartes aura*)
Goshawk (*Accipiter gentilis*)
Cooper's Hawk (*A. cooperii*)
Sharp-shinned Hawk (*A. striatus*)
Red-tailed Hawk (*Buteo jamaicensis*)
Red-shouldered Hawk (*B. lineatus*)
Broad-winged Hawk (*B. platypterus*)
Peregrine Falcon (*Falco peregrinus*)
Merlin (*F. columbarius*)
Spruce Grouse (*Canachites canadensis*)
Ruffed Grouse (*Bonasa umbellus*)
American Woodcock (*Philohela minor*)
Mourning Dove (*Zenaida macroura*)
Yellow-billed Cuckoo (*Coccyzus americanus*)
Black-billed Cuckoo (*C. erythropthalmus*)
Great Horned Owl (*Bubo virginianus*)
Long-eared Owl (*Asio otus*)
Barred Owl (*Strix varia*)
Saw-whet Owl (*Aegolius acadicus*)
Common Nighthawk (*Chordeiles minor*)
Whip-poor-will (*Caprimulgus vociferus*)
Chimney Swift (*Chaetura pelagica*)
Ruby-throated Hummingbird (*Archilochus colubris*)
Belted Kingfisher (*Megaceryle alcyon*)
Common Flicker (*Colaptes auratus*)
Pileated Woodpecker (*Dryocopus pileatus*)
Red-bellied Woodpecker (*Melanerpes carolinus*)
Red-headed Woodpecker (*M. erythrocephalus*)
Yellow-bellied Sapsucker (*Sphyrapicus varius*)
Hairy Woodpecker (*P. pubescens*)
Downy Woodpecker (*P. villosus*)
Black-backed 3-toed Woodpecker (*P. arcticus*)
Northern 3-toed Woodpecker (*P. tridactylus*)
Eastern Kingbird (*Tyrannus tyrannus*)
Great Crested Flycatcher (*Myiarchus crinitus*)
Eastern Phoebe (*Sayornis phoebe*)
Acadian Flycatcher (*Empidonax virescens*)
Yellow-bellied Flycatcher (*E. flaviventris*)
Alder Flycatcher (*E. trailli*)
Least Flycatcher (*E. minimus*)
Eastern Pewee (*Contopus virens*)
Olive-sided Flycatcher (*Nuttalornis borealis*)
Tree Swallow (*Iridoprocne bicolor*)
Blue Jay (*Cyanocitta cristata*)
Gray Jay (*Perisoreus canadensis*)
Common Raven (*Corvus corax*)
Common Crow (*C. brachyrhynchus*)
Black-capped Chickadee (*Parus atricapillus*)
Carolina Chickadee (*P. carolinensis*)
Boreal Chickadee (*P. hudsonicus*)
Tufted Titmouse (*P. bicolor*)
White-breasted Nuthatch (*Sitta carolinensis*)
Red-breasted Nuthatch (*S. canadensis*)
Brown Creeper (*Certhia familiaris*)
House Wren (*Troglodytes aedon*)
Winter Wren (*T. troglodytes*)
Bewick's Wren (*Thryomanes bewickii*)
Carolina Wren (*Thryothorus ludovicianus*)
Mockingbird (*Mimus polyglottus*)
Gray Catbird (*Dumetella carolinensis*)
Brown Thrasher (*Toxostoma rufum*)
American Robin (*Turdus migratorius*)
Wood Thrush (*Hylocichla mustelina*)
Hermit Thrush (*Catharus guttata*)
Swainson's Thrush (*C. ustulata*)
Gray-cheeked Thrush (*C. minima*)
Veery (*C. fuscescens*)
Eastern Bluebird (*Sialia sialis*)
Blue-gray Gnatcatcher (*Polioptila caerulea*)
Golden -crowned Kinglet (*Regulus satrapa*)
Ruby-crowned Kinglet (*R. calendula*)
Cedar Waxwing (*Bombycilla cedorum*)
Starling (*Sturnus vulgaris*)
Solitary Vireo (*Vireo solitarius*)
White-eyed Vireo (*V. griseus*)
Bell's Vireo (*V. belii*)
Yellow-throated Vireo (*V. flavifrons*)
Red-eyed Vireo (*V. olivaceus*)
Philadelphia Vireo (*V. philadelphicus*)
Warbling Vireo (*V. gilrus*)
Black-and-white Warbler (*Mniotilta varia*)
Prothonotary Warbler (*Protonotaria citrea*)
Worm-eating Warbler (*Helmitheros vermivorus*)
Golden-winged Warbler (*Vermivora chrysoptera*)
Blue-winged Warbler (*V. pinus*)
Tennessee Warbler (*V. peregrina*)
Nashville Warbler (*V. ruficapilla*)
Northern Parula Warbler (*Parula americana*)
Yellow Warbler (*Dendroica petechia*)
Magnolia Warbler (*D. magnolia*)
Cape May Warbler (*D. tigrina*)
Yellow-rumped Warbler (*D. coronata*)
Black-throated Green Warbler (*D. virens*)
Black-throated Blue Warbler (*D. caerulescens*)
Cerulean Warbler (*D. cerulea*)
Blackburnian Warbler (*D. fusca*)
Chestnut-sided Warbler (*D. pensylvanica*)
Bay-breasted Warbler (*D. castanea*)
Blackpoll Warbler (*D. striata*)
Pine Warbler (*D. pinus*)
Prairie Warbler (*D. discolor*)
Palm Warbler (*D. palmorum*)
Ovenbird (*Seiurus aurocapillus*)
Northern Waterthrush (*S. noveboracensis*)
Louisiana Waterthrush (*S. motacilla*)
Common Yellowthroat (*Geothlypis trichas*)
Yellow-breasted Chat (*Icteria virens*)
Mourning Warbler (*Oporornis philadelphia*)
Connecticut Warbler (*O. agilis*)
Hooded Warbler (*Wilsonia citina*)
Wilson's Warbler (*Wilsonia pusilla*)
Canada Warbler (*W. canadensis*)
American Redstart (*Setophaga ruticilla*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Brewer's Blackbird (*Euphagus cyanocephalus*)
Common Grackle (*Quiscalus quiscala*)
Brown-headed Cowbird (*Molothrus ater*)
Orchard Oriole (*Icterus spurius*)
Northern Oriole (*I. galbula*)
Scarlet Tanager (*Piranga olivacea*)
Northern Cardinal (*Cardinalis cardinalis*)
Rose-breasted Grosbeak (*Pheuticus ludovicianus*)
Evening Grosbeak (*Hesperiphona vespertina*)
Indigo Bunting (*Passerina cyanea*)
Purple Finch (*Carpodacus purpureus*)

APPENDIX I (continued)

Pine Grosbeak (*Pinicola enucleator*)
Common Redpoll (*Carduelis flammea*)
Pine Siskin (*C. pinus*)
American Goldfinch (*C. tristis*)
Red Crossbill (*Loxia curvirostra*)
White-winged Crossbill (*L. leucoptera*)
Vesper Sparrow (*Pooecetes gramineus*)
Rufous-sided Towhee (*Pipilo erythropthalmus*)
Dark-eyed Junco (*Junco hyemalis*)
Tree Sparrow (*Spizella arborea*)
Chipping Sparrow (*S. passerina*)
Field Sparrow (*S. pusilla*)
White-throated Sparrow (*Zonotrichia albicollis*)
Fox Sparrow (*Passerella iliaca*)
Swamp Sparrow (*Melospiza georgiana*)
Song Sparrow (*M. melodia*)

AVIAN COMMUNITIES: APPROACHES TO DESCRIBING THEIR HABITAT ASSOCIATIONS

Gerald J. Niemi

Lee Pfannmuller[1]

Abstract.--Four approaches are presented which enable wildlife managers to consider many avian species simultaneously in management objectives. The northeastern Minnesota avifauna is used to test each approach. Three approaches included the classification of avian species into structural successional stages, life forms, or their sociological associations. The fourth approach, habitat niche, depicts species response to quantitative habitat variables. The background, methods, data analysis, interpretation, and advantages/disadvantages of each approach are discussed.

INTRODUCTION

Wildlife managers are faced with the difficult task of predicting the impacts of habitat alterations on wildlife species. Historically, their predictions have been based on empirical data or broadly defined "animal communities." During the last ten to fifteen years, however, the ease of assimilating and integrating large quantities of data by computer has broadened the range of techniques available for modeling natural systems. Our objective is to define and describe four management approaches that are currently available to managers for modeling bird populations. We will briefly discuss the background, methods, data analysis, interpretation, and major advantages and disadvantages of each approach. Hopefully, these discussions will provide recommendations for guiding the future direction of non-game bird management.

The four approaches considered in the following pages are:

Successional Stages - a simplistic approach that identifies the bird species associated with forest types along successional gradients.

Life Form Associations - a multi-level approach that identifies assemblages of species with similar reproductive and feeding strategies.

Species Associations - a multivariate approach that identifies species with similar distributions across a range of defined communities.

Habitat Niche Analysis - a multivariate approach that assumes species occupy a mathematically definable habit hyperspace.

Each approach was utilized in an attempt to model songbird populations from northeastern Minnesota. The successional stage and life form models were examined with data from published reports, our own unpublished data, and empirical data. The species association model was modified from the work of Pfannmuller (1979), while the habitat niche model was modified from the work of Niemi (1977).

Natural Setting

The glacially-influenced landforms of northeastern Minnesota (Wright and Watts 1969; Olcott and Siegal 1978) support a rich mosaic of upland and lowland forests (Ohmann and Ream 1971; Grigal and Ohmann 1975; Dean 1971). Throughout the region glacially deposited features such as end moraines, drumlin fields and glacial lake beds dominate the terrain. This topographical diversity is reflected by similar diversity among vegetation cover types. Located in an ecotone between the northern boreal forests and the eastern deciduous forests of North America, the transitional plant communities of northeastern Minnesota have been described by several plant ecologists since Cooper's (1913) original work on Isle Royale.

The original vegetation of northeastern Minnesota consisted of a complex mosaic of red pine (Pinus resinosa), jack pine (Pinus banksiana), and white pine (Pinus strobus) forests, lack spruce (*Picea mariana*) and tamarack *Larix laricina*) bogs, and forests of pioneer ardwoods. The latter consisted primarily of uaking aspen (*Populus tremuloides*) and paper irch (*Betula papyrifera*) and, in the more ature stands, balsam fir (*Abies balsamea*). aintained primarily by lightning-induced ires and insect epidemics, these early ommunities were dominated by disturbance-dapted species (Heinselman 1973; Ahlgren 975; Grigal and Ohmann 1975). Because isturbance was a frequent natural occurence prior to man's intervention, a true stable climax' may rarely have developed Heinselman 1973).

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Today, logging activities generally eplace natural disturbance as the method f stand renewal. Although the glacially-coured and fire-controlled terrain of ortheastern Minnesota was originally quite eterogeneous, man's activities have added o the disturbed and patchy nature of the orest.

The vegetational diversity that is haracteristic of this region is an important nfluence upon the size and diversity of vian populations. The limited number of ensity estimates that have been reported for reeding populations in the area (Green et al. 978) are considerably higher than values eported from similar cover types in Canada Erskine 1977). Minnesota estimates range rom approximately 500 pairs/km^2 in recent learcuts and stunted conifer bogs to 000-1500 pairs/km^2 in wetland shrub stands. ven the highest breeding densities reported n Canada rarely exceeded 500-600 pairs/km^2. everal factors may be responsible for this iscrepancy. First, the method for deterining the number of territorial males per lot was more conservative in the studies y Erskine (1977). Second, many study plots n Minnesota were small; ranging from 2 to ha in size, while study plots in Canada ere a minimum of 16 ha in size. The influnce of plot size upon population estimates as been noted by Oelke (1966). The differnce in plot size, however, reflects an mportant difference between the forests of anada and Minnesota. Large, continuous tands of homogeneous cover types, common n Canada, are rare in the disturbed forests f northeastern Minnesota.

Minnesota's northeastern forests are lso characterized by a rich diversity of reeding species. Unlike the rest of the tate where members of the blackbird family Icteridae) dominate the avifauna, wood arblers (Parulidae) contribute the largest ercentage of both individuals and species o the summer avifauna of northeastern Minnesota (Fig. 1). Other important passerine families include the sparrows, grosbeaks and finches (Fringillidae) with approximately 15 breeding species, the tyrant flycatchers (Tyrannidae) with approximately 8 breeding species, and the thrushes (Turdidae) with approximately 5 breeding species (Green and Janssen 1975). Several species found in our northeastern forests are typically classified as boreal species and are quite rare in the continental United States. These include the black-backed three-toed woodpecker, spruce grouse, goshawk and boreal owl (Green and Janssen 1975). The habitat requirements of these species may deserve the special attention of wildlife managers in areas with a boreal element.

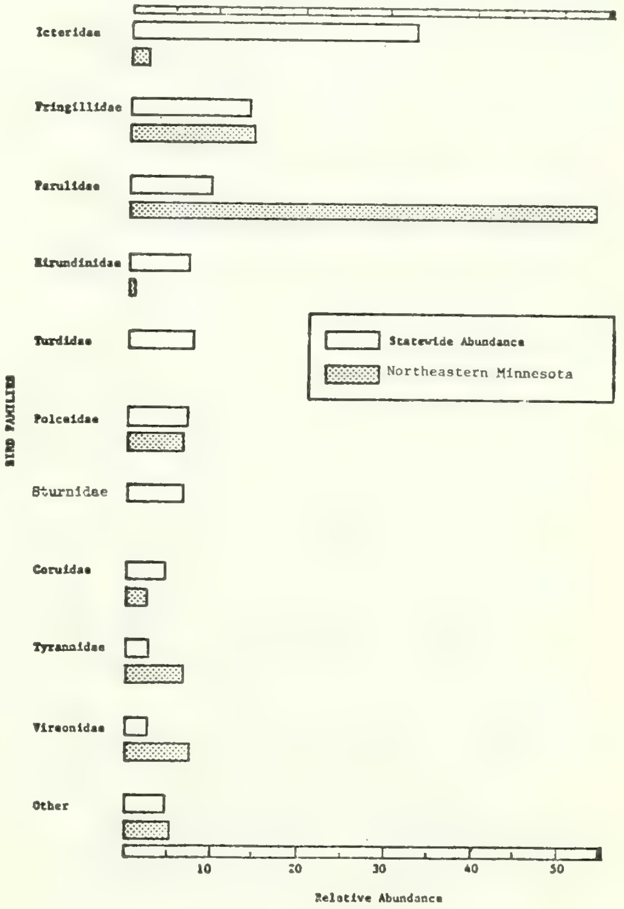


Figure 1.--The relative abundance of major passerine bird families in the State of Minnesota compared with northeastern Minnesota.

Data for this paper were drawn largely from two major studies conducted in northeastern Minnesota. One was conducted in an area of extensive taconite development located east of the mining towns of Hoyt Lakes and Babbitt, Minnesota (Pfannmuller 1979). The second study was conducted in an area within and surrounding the 1971 Little Sioux burn, located approximately 20 miles northwest of Ely, Minnesota and near the Island Lake Reservoir, approximately 20 miles north of Duluth, Minnesota (Niemi 1977). Other studies from which data were drawn include Todd and Doran (1976), Green et al. (1978), Bergstedt and Neimi (1974), and Green (1971a).

Bird Species and Data Base

Because more than 250 species of birds are known to occur in northeastern Minnesota, we felt it was practical to limit the number of species considered in this paper. We defined our data base by including only terrestrial species that are summer residents. Terrestrial species were arbitrarily defined as species found in communities ranging from the cattail-sedge marshes (where standing vegetation is present all year) to the drier upland forests. Thus, we excluded species found in the emergent aquatic marshes (where vegetation is present throughout much of the year) and open water areas. Species were further excluded if they could be classified into one of the following four categories:

1. Man-adapted species found commonly near settlements, towns, and cities;
2. Species with specific habitat or niche requirements;
3. Species in which we lack sufficient data; and/or
4. Species in northeastern Minnesota that are on the limit of their breeding range.

The species data base and the classification criteria are shown in table 1.

The concept of excluding species may seem contradictory to multiple species management. However, limiting the number of species in management models is appropriate if the limitations are based on sound rationale. For example, should species found in association with man's settlements be managed in forest ecosystems? Many of these species are much more abundant today than they were in pre-settlement times (Graber and Graber 1963). Species with specific habitat requirements may require special management strategies, especially if those requirements are limited in their availability. Species for which we are lacking data are particularly important. These species should be given research priority in order to determine their habitat requirements and to determine if their population levels are stable or declining. Finally, managing species on the limits of their range may not benefit the species and their inclusion could negatively influence species indigenous to an area.

One of the primary reasons for defining a species base was to focus attention on species that were particularly dependent on vegetational communities in northeastern Minnesota. Since the data base was established after both the habitat niche and species association analyses were completed, some species that were excluded from the data base, may be included in subsequent tables and figures.

SUCCESSIONAL STAGE APPROACH

Background

The general concept that birds select habitats based on the vegetation structure or habitat physiognomy has been expressed by several researchers (e.g., Lack 1933; Odum 1950; Svardson 1949; Hinden 1965; James 1971). Since succession has been described as an orderly process involving changes in the "structure" of habitats (Odum 1959), it seems natural to classify bird species into communities that are based on the structural categories found along successional gradients. In light of the relationship between bird species and successional stages, it is surprising to note that there are few systematic inventories of the birds inhabiting various stages. Erskine (1977), after discussing the birds of various forest types, comments as follows, "the need for systematic data on birds of successional and edge habitats could hardly be made more obvious." Nevertheless, some pertinent data are available in Kendeigh (1945) Johnston and Odum (1956), Martin (1960), Haapanen (1965), Shugart and James (1973), Holt (1974), and Erskine (1977).

Method

We defined a series of 11 forest types which are the predominant cover types found in northeastern Minnesota. They are described as follows:

Grassland-forbaceous - An open upland area that lacks trees and shrubs. The flora is composed of grasses (Gramineae spp.) and a wide assortment of "weeds" standing up to 1 m high. The cover type is limited and occurs only in early clearcuts, intensely burned areas, or settlements.

Table1 .--Bird species data base for northeastern Minnesota. Species list includes those considered to be summer residents excluding waterbirds such as loons, grebes, ducks, coot, gulls, and terns as adapted from the annotated list in Green et al. (1978).

CLASSIFICATION CRITERIA 1/

SPECIES	INCLUDED IN ANALYSIS	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Double-crested Cormorant			X		
Great Blue Heron			X		
American Bittern	X				
Turkey Vulture				X	
Goshawk				X	
Cooper's Hawk				X	X
Sharp-shinned Hawk				X	
Red-tailed Hawk	X				
Broad-winged Hawk	X				
Bald Eagle			X		
Marsh Hawk	X				
Osprey			X		
Merlin				X	
American Kestrel	X				
Spruce Grouse	X				
Ruffed Grouse	X				
Sandhill Crane				X	
Virginia Rail					X
Sora	X				
Killdeer		X			
American Woodcock	X				
Common Snipe	X				
Upland Plover					X
Spotted Sandpiper			X		
Mourning Dove		X			X
Black-billed Cuckoo					X
Great Horned Owl				X	
Barred Owl				X	
Long-eared Owl				X	
Short-eared Owl				X	
Common Nighthawk		X			
Chimney Swift		X			
Ruby-throated Hummingbird			X		
Belted Kingfisher			X		
Common Flicker	X				
Pileated Woodpecker	X				
Red-headed Woodpecker					X
Yellow-bellied Sapsucker	X				
Hairy Woodpecker	X				
Saw-whet Owl				X	
Whip-poor-will					X
Downy Woodpecker	X				
Black-backed 3-toed Wood				X	
Eastern Kingbird	X				
Great-crested Flycatcher					X
Eastern Phoebe			X		
Yellow-bellied Flycatcher	X				
Alder Flycatcher	X				
Least Flycatcher	X				
Eastern Wood Pewee	X				
Olive-sided Flycatcher	X				
Tree Swallow	X				
Bank Swallow			X		
Rough-winged Swallow			X		

Table 1.--Continued

SPECIES	INCLUDED	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Barn Swallow		X	X		
Cliff Swallow		X	X		
Purple Martin		X			
Gray Jay	X				
Blue Jay		X			
Common Raven			X	X	
Common Crow		X			
Black-capped Chickadee	X				
Boreal Chickadee	X				
White-breasted Nuthatch					X
Red-breasted Nuthatch	X				
Brown Creeper			X	X	
House Wren		X			
Winter Wren				X	
Short-billed Marsh Wren	X				
Catbird	X				
Brown Thrasher	X				
Robin		X			
Wood Thrush					X
Hermit Thrush	X				
Swainson's Thrush	X				
Veery	X				
Eastern Bluebird			X		
Golden-crowned Kinglet	X				
Ruby-crowned Kinglet	X				
Cedar Waxwing		X			
Starling		X			
Solitary Vireo	X				
Red-eyed Vireo	X				
Philadelphia Vireo				X	
Warbling Vireo		X			
Black & White Warbler	X				
Golden-winged Warbler					X
Tennessee Warbler				X	
Nashville Warbler	X				
Parula Warbler	X				
Yellow Warbler		X			
Magnolia Warbler	X				
Cape May Warbler	X				
Yellow-rumped Warbler	X				
Blk-throated Green Warbler	X				
Blackburnian Warbler	X				
Chestnut-sided Warbler	X				
Bay-breasted Warbler	X				
Pine Warbler				X	
Palm Warbler				X	
Ovenbird	X				
Northern Waterthrush			X		
Connecticut Warbler	X				
Mourning Warbler	X				
Yellowthroat	X				
Wilson's Warbler				X	
Canada Warbler	X				
American Redstart	X				
House Sparrow		X			
Bobolink		X			
Eastern Meadowlark		X			

Table 1.--Continued

SPECIES	INCLUDED	URBAN ADAPTED	SPECIAL NEEDS	LACK OF DATA	RANGE LIMIT
Western Meadowlark		X			
Yellow-headed Blackbird					X
Redwinged Blackbird		X			
Baltimore Oriole		X			X
Rusty Blackbird				X	X
Brewers Blackbird		X			
Common Grackle		X			
Brown-headed Cowbird		X			
Scarlet Tanager	X				
Rose-breasted Grosbeak	X				
Evening Grosbeak	X				
Purple Finch	X				
Pine Siskin				X	
American Goldfinch	X				
Red Crossbill				X	
White-winged Crossbill				X	
Savannah Sparrow		X			
Vesper Sparrow		X			
Dark-eyed Junco	X				
Chipping Sparrow	X				
Clay-colored Sparrow					X
White-throated Sparrow	X				
Lincoln's Sparrow	X				
Swamp Sparrow	X				
Song Sparrow		X			

TOTAL SPECIES

1/ See text for explanation.

Cattail-sedge marsh - An open, wet area that lacks trees and shrubs. The flora is composed primarily of cattails (*Typhaceae*) and sedges (*Cyperaceae*) standing up to 2 m high. The cover type has a limited distribution in northeastern Minnesota.

Heath muskeg bog - An open lowland area that lacks trees; shrubs are rarely present. The flora is composed primarily of heath species (*Ericaceae*) standing up to 1 m high. The cover type is common in northeastern Minnesota.

Young open shrub - An upland shrub with scattered dead and/or live trees. Structurally, the habitat consists of a dense shrub layer, up to 3 m high, and a well-developed herbaceous layer. The flora may be composed of deciduous saplings such as quaking aspen, paper birch, or shrub species such as hazel (*Corylus cornuta*) or juneberry (*Amelanchier spp*.). The cover type is very common and is present within 3 to 12 years following logging or forest fire.

Wetland shrub - A lowland shrub area with scattered live and/or dead trees. Structurally the habitat consists of a dense shrub layer, approximately 3 m high and a variable herbaceous layer. The dominant floral species are alder (*Alnus rugosa*) and willow (*Salix spp*.). The cover type is quite common.

Young deciduous - An upland, medium-aged, tree stand with variable shrub and herbaceous layers. Structurally, the vegetation consists of a dense, deciduous tree layer, ranging from 3 to 9 m high. The typical tree species are quaking aspen and paper birch. The cover type is common 12 to 30 years following forest fire or logging.

Young coniferous - An upland, medium-aged, tree stand with sparse shrub and herbaceous layers. Structurally the vegetation consists of a dense coniferous tree layer, ranging from 3 to 9 m high. The typical tree species may be jack pine, red pine, white pine, white spruce (*Picea glauca*) or balsam fir. The cover type is common 12 to 30 years following forest fire or logging.

Semi-open conifer lowland - A stand whose structure is intermediate between that of the heath muskeg bog and the mature lowland conifer bog. Structurally the vegetation consists of a dense, low-lying heath layer, up to 1 m high, and a low to moderately dense tree layer up to 6 m high. The tree species are usually black spruce or tamarack. The cover type is fairly common.

Mature deciduous upland - A closed-canopy, deciduous upland stand with a moderate to dense tree layer, ranging from 9 to 20 m high, and a variable shrub and herbaceous layer. The tree species are usually quaking aspen or paper birch, although northern hardwoods (e.g., maple and basswood) may predominate near Lake Superior. The cover type is very common.

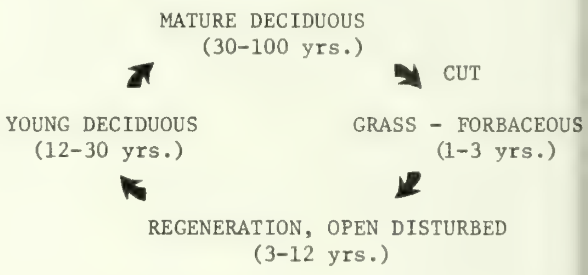
Mature coniferous upland - A closed-canopy, coniferous upland stand with a moderate to dense tree layer, ranging from 9 to 20 m high, and a sparse shrub and herbaceous layer. The tree species may include red pine, jack pine, white pine, white spruce, or balsam fir. The cover type is common and is often an actively-managed community.

Mature conifer lowland - A closed-canopy, coniferous lowland stand with a moderate to dense tree layer, up to 20 m high, a sparse shrub layer, and a dense herbaceous layer (comprised of moss and heath species). The tree species are usually black spruce or tamarack or occasionally white cedar (*Thula occidentalis*). The cover type is very common.

Bird species were then classified into one or more of these 11 cover types, depending on their use of each habitat for either reproduction and/or feeding. Data were extracted from a variety of sources including Pfannmuller (1979), Green and Niemi (1977), Todd and Doran (1976), Bergstedt and Niemi (1974), Green (1971a), field experience, or consultation with local experts.

Data Analysis and Interpretation

The results of the classification are shown in Table 2. The table provides a framework for modeling the habitat distributions of bird species in northeastern Minnesota. Using these data, the manager can predict some of th impacts of habitat alteration. For example, the following successional sequence would result if a mature deciduous forest were cut:



The rotation of species through this deciduous sere could be approximated from the informatio in Table 2.

As shown in Table 2, there is a general pattern of increasing number of species from the grass-forb type to the mature deciduous upland. Since the grass-forb and cattail-sedge types are the least complex (essentially one-layered) and the mature deciduous upland is the most complex (multi-layered), this increase generally reflects the complexity of the vegetation. The young open shrub and wetland shrub types are intermediate in structural complexity and the number of species generally associated with these types are also intermediate. However, if the number of dead or live trees is substantial in these types, then the numbers of bird species and individuals can also be quite high.

Advantages

1. The approach provides a *baseline* to build more sophisticated and realistic models for predicting the impacts of forest management.
2. The successional types are easily interpreted by most users.
3. The model permits the manager to make broad generalizations regarding the impact of forest management on nongame birds.

Table 2.--Life form association, successional stages used for reproduction (X), feeding (O), and adaptability index for the bird species data base defined in Table 1.

SPECIES	Life form 1/	Grass-Forb	Cattail-Sedge	Muskeg Bog	Young Open Shrub 2/	Young Deciduous	Young Coniferous	Mature (upland) Deciduous	Mature Coniferous Upland	Semi-Open Conifer Lowland	Mature Conifer Lowland	Wetland Shrub	ADAPTABILITY 3/ Total X	Total O	Index
American Bittern	3		X O	X O									2	2	3
Red-tailed Hawk	9	O			X O			X					2	2	3
Broad-winged Hawk	11	O			O			X O					1	3	2.5
Marsh Hawk	5	O	X O	X O	O								2	4	4
American Kestrel	14	O			X O								1	2	2
Spruce Grouse	10			X					X O	X	X O		4	2	5
Ruffed Grouse	5				X O	X O		X O					3	3	4.5
Sora	3		X O									X O	2	2	3
American Woodcock	3,5	X	O		X	X	X					X O	5	2	6
Common Snipe	3	X	X O	X O								X O	4	3	5.5
Common Flicker	13	O			X O			X					2	2	3
Pileated Woodpecker	13							X O					1	1	1.5
Yellow-bellied Sapsucker	13							X O	X O				2	2	3
Hairy Woodpecker					X O			X O					2	2	3
Downy Woodpecker	13				X O	X O		X O				O	3	3	4.5
Eastern Kingbird	8,11	X O			X O							X O	3	3	4.5
Yellow-bellied Flycatcher	6								X O	X O	X O		3	3	4.5
Alder Flycatcher	8				X O							X O	2	2	3
Least Flycatcher	8,11					X O		X O	X O				3	3	4.5
Eastern Wood Pewee	8,11							X O	X O				2	3	3
Olive-sided Flycatcher	8,11				X O					X O		X O	3	3	4.5
Tree Swallow	14	X O		X O	X O					X O			4	4	6
Gray Jay	10								X O	X O	X O		3	3	4.5
Black-capped Chickadee	14					X O	X O	X O					3	3	4.5
Boreal Chickadee	14								X O	X O	X O		3	3	4.5
Red-breasted Nuthatch	14							X O	X O		X O		3	3	4.5
Short-billed Marsh Wren	3,6,8	X O	X O	X O									3	3	4.5
Catbird	5,6,7,8				X O							X O	2	2	3
Brown Thrasher	5,6,7,8				X O							X O	2	2	3
Hermit Thrush	5					X O	X O	X O	X O	X O	X O		6	6	9
Swainson's Thrush	7,8								X O	X O	X O		3	3	4.5
Veery	5,6				X O	X O		X O					3	3	4.5
Ruby-crowned Kinglet	10							X O		X O			2	2	3
Golden-crowned Kinglet	10							X O		X O			2	2	3
Solitary Vireo	8,11						X O	X O		X O			3	3	4.5
Red-eyed Vireo					X O	X O		X O					3	3	4.5
Black and White Warbler	6				X O	X O		X O	X O	X O		X O	6	6	9

Table 2.--continued

SPECIES	Life Form	Grass-Forb	Cattail-Sedge	Muskeg Bog	Young Open Shrub	Young Deciduous	Young Coniferous	Mature Deciduous Upland	Mature Coniferous Upland	Semi-open Coniferous Lowland	Mature Conifer Lowland	Wetland Shrub	ADAPTABILITY		
													Total X	Total O	Index
Nashville Warbler	6						X O	X O[4]	X O	X O	X O		5	5	7.5
Parula Warbler	11							X O[4]	X O		X O		3	3	4.5
Magnolia Warbler	8,10,11						X O	X O[4]			X O		3	3	4.5
Cape May Warbler	10									X O	X O		2	2	3
Yellow-rumped Warbler	10						X O	X O[4]	X O	X O	X O		5	5	7.5
Black-throated Green Warbler	8,10,11							X O[4]					1	1	1.5
Blackburnian Warbler	10								X O		X O		1	1	1.5
Chestnut-sided Warbler	8				X O	X O	X O	X O				X O	5	5	7.5
Bay-breasted Warbler	10,11									X O	X O		2	2	3
Ovenbird	5					X O	X O	X O	X O				4	4	6
Connecticut Warbler	6								X O	X O	X O		3	3	4.5
Mourning Warbler	6,8				X O	X O	X O						3	3	4.5
Yellowthroat	3,6,8		X O	X O						X O		X O	4	4	6
Canada Warbler	6,8					X O		X O	X O				3	3	4.5
American Redstart	8,9,11					X O		X O				X O	3	3	4.5
American Goldfinch	5,6,7,8	X O			X O							X O	3	3	4.5
Purple Finch	10,11								X O				1	1	1.5
Scarlet Tanager	9,11							X O					1	1	1.5
Evening Grosbeak	10,11				X O		X O		X O		X O		4	4	6
Rose-breasted Grosbeak	8,9,11					X O		X O					2	2	3
Dark-eyed Junco	5						X O		X O	X O	X O		4	4	6
Chipping Sparrow	7,8,10,11						X O		X O	X O	X O		4	4	6
White-throated Sparrow	5,6					X O	X O	X O	X O	X O	X O	X O	8	8	12
Lincoln's Sparrow	5,6				X O					X O	X O		3	3	4.5
Swamp Sparrow	3,6,8		X O	X O						X O	X O		4	4	6
Total species feeding		9	8	8	23	16	12	27	25	17	21	18			
Total species reproducing		6	7	9	22	17	13	29	25	18	21	17			

[1] Life form categories as defined in table 3.

[2] Snags or live trees are necessary for some species classified in this type.

[3] Index calculated by [2 (Reproduction stages) + Feeding stages] / 2.

[4] Species generally

Disadvantages

1. Since systematic data is often lacking to quantify the species population levels within each successional range and to pinpoint the range of habitats occupied by each species, we were forced to make subjective judgements regarding a species classification. Such judgements are always prone to individual bias.
2. The approach also forces a subjective judgement of habitat classification when habitats themselves are difficult to classify. Obviously one may define more than 11 forest types in northeastern Minnesota. Many habitats, for example, are mixed associations resulting from such events as forest fire, logging, insect infestation, or natural disasters. Few forest stands are homogeneous cover types.
3. Realistically, we believe the successional approach is too simplistic and does not account for many factors that are important to the distribution of individual species.

LIFE FORM APPROACH

ackground

The life form approach to wildlife anagement was recently introduced by wild-ife biologists and foresters working in he Blue Mountains of northeastern Oregon nd Washington (Thomas et al. 1975, Thomas t al. 1976). The approach was an attempt o develop a management model broad enough o be applicable to all vertebrate species nd yet detailed enough to consider pecies-specific management issues. An dditional criterion focused on the ability f the model to relate directly to present ilvicultural practices. Because demands or timber production currently guide nearly ll facets of forest management, it was mportant for wildlife managers to incor-orate forestry concepts in their manage-ent models. Together these considerations ed to the development of the life form pproach to species management.

Similar to the guild concept used by vian ecologists (Salt 1957; Cody 1974), he life form is defined as an assemblage f species with similar reproductive and feeding strategies. For example, all birds that nest in shrubs and feed on the ground would be considered as belonging to one life form. The utility of the approach is based on the premise that species with similar habitat requirements will generally respond in a similar manner to habitat alterations. If shrubs were removed from a forest stand one would no longer expect to find shrub nesting species.

Alterations to the habitat are interpreted as changes that will either advance or retard a plant community's rate of succession. Logging, for example, will revert an upland stand back to a young herb-dominated community. A life form's response to such alterations represents the average response of all species within the particular life form category. A species response, in turn, is determined by examining its utilization of the major habitat types and successional stages in the region of interest. By summarizing the response of different species, the life form approach permits the wildlife manager and forester to manage for many species simultaneously, rather than the cumbersome task of initially having to consider each species separately. If needed, the data are also available for predicting the response of individual species.

Thomas and his co-workers considered several other factors in their life form model, such as a species use of special and/or unique habitats. A vulnerability index was also calculated to determine a species (or life form's) degree of adaptability or vulnerability to habitat manipulation.

Methods

We used the sixteen life form categories that Thomas et al. (1976) defined for their work in the Blue Mountains (table 3). The category or categories to which each bird species was assigned is shown in Table 2.

Each species utilization of plant communities in northeastern Minnesota was also determined (Table 2). Unlike the model of Thomas et al. (1975) which dealt separately with a species use of timber types and with its use of successional stages, we attempted to combine these responses by considering the eleven structural communities we previously defined. One reason we eliminated this separation was due to the small age spread for upland habitats in northeastern Minnesota and the corresponding lack of bird data across such fine categories.

Table 3. Life Form Definitions.1/

Life Form 1:	Reproduces in the water and feeds in the water.
Life Form 2:	Reproduces in the water and feeds on the ground, in bushes or in trees.
Life Form 3:	Reproduces on the ground around water, feeds on the ground, in bushes or in water.
Life Form 4:	Reproduces on or in cliffs, caves, rim and talus slopes, feeds on the ground or in the air.
Life Form 5:	Reproduces on the ground, without specific water, cliff, rim or talus association, and feeds on the ground.
Life Form 6:	Reproduces on the ground, feeds in bushes and trees or in the air.
Life Form 7:	Nests in bushes, feeds on the ground, in water and in the air.
Life Form 8:	Nests in bushes, feeds in trees and bushes or in the air.
Life Form 9:	Nests primarily in deciduous trees, feeds in trees and bushes.
Life Form 10:	Nests primarily in conifers, feeds in trees and bushes, or in the air.
Life Form 11:	Nests in conifers or deciduous trees and feeds in trees or bushes, on the ground or in the air.
Life Form 12:	Nests on very thick branches, feeds on the ground or in water.
Life Form 13:	Excavates own hole, feeds in trees, brush or air.
Life Form 14:	Nests in a hole made by another species or in a naturally occurring hole-feeds on the ground, in water or in the air.
Life Form 15:	Reproduces in a burrow (underground) and feeds on or under the ground.
Life Form 16:	Reproduces in a burrow (underground) and feeds in the air or in the water.

1/ From Thomas *et al*. (1976)

Stands older than 60-70 years are scarce. In addition, because both upland and lowland habitats were considered in our model, we did not feel that the age boundaries nor the response of bird species for successional stages in uplands were necessarily applicable to the successional stages in lowlands.

With the bird data for each of the eleven habitats, we calculated a vulnerability index for each species (Table 2). As specified by Thomas *et al*. (1975), the index value was calculated by doubling the number of reproductive habitats the species uses, adding it to the number of feeding habitats used and dividing the sum by two. Although a species orientation to unique and or special habitats (e.g., snags, cliffs, etc.) may be included in the model, we did not incorporate such an analysis in this investigation.

Data Analysis and Interpretation

A major objective of the life form approach is to predict the response of vertebrates with similar habitat requirements to various habitat alterations. To illustrate, we examined life form 13 (species that excavate their own nesting cavities in a tree and feed either on the ground, in bushes, in trees or in the air). In northeastern Minnesota we identified eight species in life form 13 (Table 2). In addition to the woodpecker species, we have also included the boreal and black-capped chickadees. Although these chickadees may utilize either nesting cavities constructed by other species or natural cavities, they may also excavate their own (Harrison 1975). Based on the information in Table 2, the distribution of life form 13 in our eleven structural communities is shown in Figure 2. The figure provides the wildlife manager and forester with two types of information: 1) presence/absence information regarding the distribution of the life form within the communities; and 2) a means for predicting the impact of various habitat alterations. For example, the mature deciduous community satisfies the habitat requirements for a larger proportion of species in life form 13 than any other community. If a 50-year-old aspen stand were clearcut, one

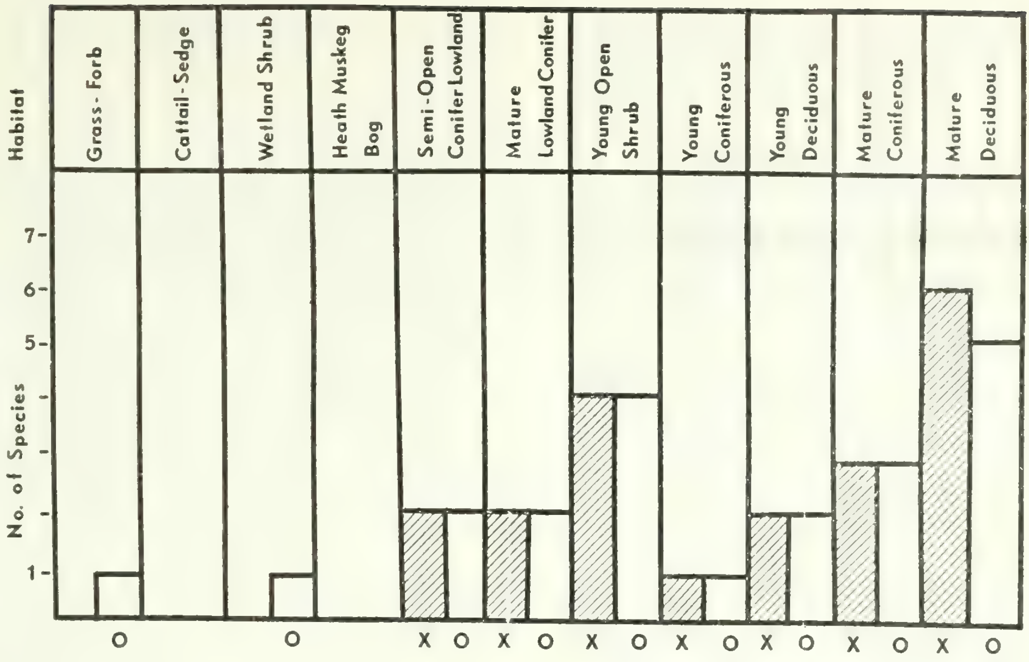


Figure 2.-- Distribution of Life Form 13 among the major habitats in northeastern Minnesota.
x= nesting 0=feeding

would predict a small decrease in the number of self-excavating cavity nesters, as long as some snags were left standing. If snags were removed, then the impact to cavity nesting species would be much greater.

Consideration of life forms provides helpful generalizations, but it is still important to consider the response of individual species. Information regarding species in life form 13 has been summarized in Table 4. An important question to consider when contemplating management alternatives is, 'Are some species within the life form more vulnerable to habitat alterations than other species?' Using the previous example, are there species within life form 13 that are so narrowly confined to the mature deciduous habitat that its loss would be detrimental to the species population in northeastern Minnesota? Our table indicates that the loss of the aspen stand might be more detrimental to the pileated woodpecker than to other species within the life form. Another important consideration is the availability of the particular habitat with regards to both time and space. Loss of a rare habitat is obviously more likely to be detrimental to a vulnerable species than the loss of an abundant habitat.

Advantages

1. The life form approach integrates the information available for each species into the framework of a single model. It's value in establishing a data base for all vertebrate species should not be overlooked.

2. Condensing species information into a "workable" number of life form categories permits the manager to consider many taxa simultaneously.

3. The life form approach is flexible enough to allow for the incorporation of new data.

4. The approach generates a "rough" index of a species (and life forms) vulnerability to habitat manipulation. Although the index is a valuable indicator for predicting species composition changes on a broad scale, neither the index, nor the entire management approach, were intended as more than initial steps when dealing with specific management problems.

Species / Habitat	Grass-Forb	Cattail-Sedge	Wetland Shrub	Heath Muskeg	Semi-open Conifer	Mature Lowland Conifer	Young open Shrub	Young Coniferous	Young Deciduous	Mature Coniferous Upland	Mature Deciduous Upland	Adaptability-Vulnerability
Common Flicker	o				x o						o	3
Pileated Woodpecker											x o	1.5
Yellow-bellied Sapsucker										x o	x o	3
Hairy Woodpecker							x o				x o	3
Downy Woodpecker							x o		x o		x o	4.5
Black-backed 3-toed Woodpecker					x o	x o	x o			x o		6.0
Black-capped Chickadee								x o	x o		x o	4.5
Boreal Chickadee					x o	x o					x o	4.5

Table 4. The distribution of species in Life Form 13 among the major habitats in northeastern Minnesota.

Disadvantages

1. The original classification of structural communities is subjective rather than objective. In addition, the biologist's decision concerning species utilization of a structural community for feeding or reproduction is also subjective. The manager must make a judgement which is subject to bias and which is based generally on a limited amount of available information.

2. When a species ecology is inadequately known, its' adaptability/vulnerability may be inaccurately judged - another reason why the model is intended only as an initial approach to impact analysis. For example, in our earlier illustration, the model predicts that the black-backed three-toed woodpecker is more adaptable to habitat alterations than other species in life form 13 - a prediction many ornithologists might dispute.

3. Many species may be classified in more than one life form category. In many cases, this probably reflects the insufficient data that is available to the ecologist, particularly with respect to feeding habits. On the other hand, the adaptability of some species is reflected by classifying them in more than one category.

MULTIVARIATE APPROACHES

One of the principal criticisms of the two approaches we presented above is their reliance on subjective judgements. Although these judgements were based on field experience and familiarity with the literature, a need clearly exists for more objective approaches to modeling natural systems. Such concern has prompted avian ecologists (e.g., James 1971; Whitmore 1977; Smith 1977) to investigate various multivariate approaches to avian community analysis. Multivariate techniques were implemented in the species association approach described below in order to analyze the relationships among species and in the habitat - niche analysis to analyze the relationships between species and their environment.

SPECIES ASSOCIATIONS AND AVIAN COMMUNITIES

Background

The following approach to community analysis implements multivariate techniques to classify avian communities and to delineate species associations within those communities. As we stated earlier, the classification of avian communities has, historically, been rather subjective (e.g., Kendeigh 1945; Martin 1960). Most avian ecologists have assumed that the "boundaries" of avian communities directly reflect the "boundaries" of plant communities. Though the plant community framework is satisfactory for a preliminary assessment, the wildlife manager should not assume that the same boundaries always apply to avian communities. Our intent was to derive a classification scheme for bird communities with the use of parameters that quantified the bird species composition rather than the plant species composition. Compared with the numerous studies using rigorous mathematical approaches to plant community classification (e.g., Grigal and Ohmann 1975; Nobles _et_ _al_. 1977), few studies have dealt with such an approach to avian community classification.

The second objective of the association approach was to delineate species associations; a species association being a group of species that are distributed in a similar manner among avian communities. Few species, either plant or animal, are restricted in their occurrence to one community. Several species may often occur together in different communities because they require a similar environmental feature. Our objective was to characterize the bird species associations in northeastern Minnesota and to illustrate their occurrence and abundance within the different avian communities.

We chose cluster analysis (Boesch 1977; Pielou 1977) as the mathematical technique for defining avian communities and associations. The technique operates by combining sets of data, or entities, on the basis of their overall similarity. In this example the 'sets of data' corresponded to the set of avian population censuses for all study plots, while the 'entities' corresponded to each of the individual bird species. The degree of similarity among plot censuses, or among the distribution of individual species, was mathematically interpreted as the distance between sample points. The clustering process may be graphically represented by a dendogram which illustrates the hierarchial arrangement of the data sets or entities (e.g., see Cody 1974).

Cluster analysis operates under the assumption that the sample units naturally fall into discrete and recognizable communities. The validity of this assumption however, has been challenged by ecologists who allege that discrete discontinuities between communities are not realistic (e.g., Gleason 1926; Curtis 1959). Those ecologists who maintain that species are geographically distributed independently of one another favor the use of ordination techniques that graphically portray the relationships among sample stands. Ordination arranges the stands within a uni-dimensional coordinate frame so that the relative continuity or discontinuity in their distribution is illustrated. The ordination technique commonly used for this purpose is discriminant analysis. Discriminant analysis operates by defining linear combinations of the components of each stand (e.g., species) so that, within a coordinate frame, the distances between communities are maximized. In avian ecology, discriminant analysis has recently been used by several authors to graphically illustrate the distribution of individual species (James 1971; Whitmore 1977; Smith 1977; Thomas _et_ _al_. 1977). We have implemented discriminant analysis to portray the degree of similarity/dissimilarity among the species composition of the different study plots.

Methods

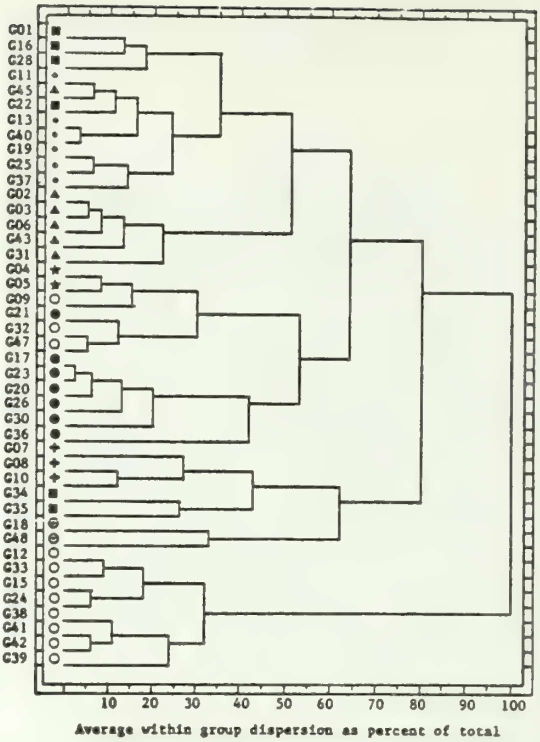
The procedures for implementing cluster analysis were applied to avian census data collected in 43 forest stands. The sample stands were selected to represent the portions of all major cover types in northeastern Minnesota. Territory mapping (Williams 1936) was selected for collecting census data from each plot during the 1977 summer season. Although we will briefly review our analysis procedures in the following paragraphs, Pfannmuller (1979) should be consulted for further details.

In order to define both the avian communities and species associations that characterize northeastern Minnesota, we needed to implement the technique of cluster analysis in two different ways. The first, referred to as normal analysis, (Boesch 1977) was used to classify communities. Normal analysis grouped together the 43 sample stands on the basis of their overall similarity in bird species composition. For example, we would predict that the bird censuses from two mature jack pine stands would be recognized as representing one avian community. Discriminant analysis was also applied to graphically portray the 'distance' or similarity in the avian composition of the sample stands. The second type of cluster analysis, referred to as inverse analysis (Boesch 1977), was used to define species associations. Inverse analysis grouped together bird species that showed similar distribution among the 43 sample stands. For example, we might predict that the red-eyed vireo and ovenbird, species that are both commonly observed in mature upland forest stands, would be members of one species association.

Computer programs designed to conduct cluster analysis were written by E.J. Cushing of the University of Minnesota and by G. Burnett, of the State of Minnesota (State Planning, Regional Copper-Nickel Study). The input variables for the program, and the distance equations for computing similarity, were systematically altered by the authors. Further details can be found in Pfannmuller (1979).

Data Analysis and Interpretation

By varying both the nature of the input variables and the distance equations, several dendrograms were generated with normal cluster analysis; one such example is shown in Figure 3. The figure clearly suggests an appropriate scheme for classification. For example, the bird species composition in eight of the eleven deciduous upland plots was recognized as similar and they were distinct from the species composition on the remaining thirty-five sample plots. It is appropriate at this point to advance a warning - the ecologist should not interpret the classification suggested by any one dendrogram as definitive. Rather, all dendrograms generated from normal analysis should be analyzed before proposing a reasonable classification (which may not directly reflect any one particular dendrogram). Based on the 1977 breeding bird data, nine avian communities were delineated for northeastern Minnesota (see Fig. 5). A graphical illustration of the similarity of their species composition is shown in Figure 4. Several dendrograms were also generated from inverse cluster analysis. Although we have not included any of the dendrograms here, the final classification of species associations is detailed in Table 5. In addition, the relative abundance of the species associations in each avian community is illustrated in Figure 5.



Key to major vegetation cover types on each plot:

- ■ **Young plantation**
- • **Recent Clearcut**
- ▲ **Conifer lowland**
- ○ **Deciduous upland**
- ★ **Disturbed shrub**
- ● **Conifer upland**
- ✦ **Aspen regeneration**
- ● **Alder**

Figure 3.--Dendrogram showing the hierarchial relationships among bird communities of 43 stands based on the density of 56 breeding bird species.

The delineation of avian communities with the use of dendrograms suggests structural features of the vegetation that are important to birds in northeastern Minnesota. For example, the avian composition of mature deciduous uplands was recognized as distinctly different from the avian composition of mature coniferous uplands. Therefore, a major structural distinction important to many species in their selection of a breeding habitat was the distinction between deciduous and coniferous vegetation. However, the distinctions between different deciduous cover types or different coniferous cover types were apparently not important to birds. The species composition of mature red pine stands, for example, were not recognized as faunistically distinct from the species composition of mature jack pine stands. The community in Figure 4 also

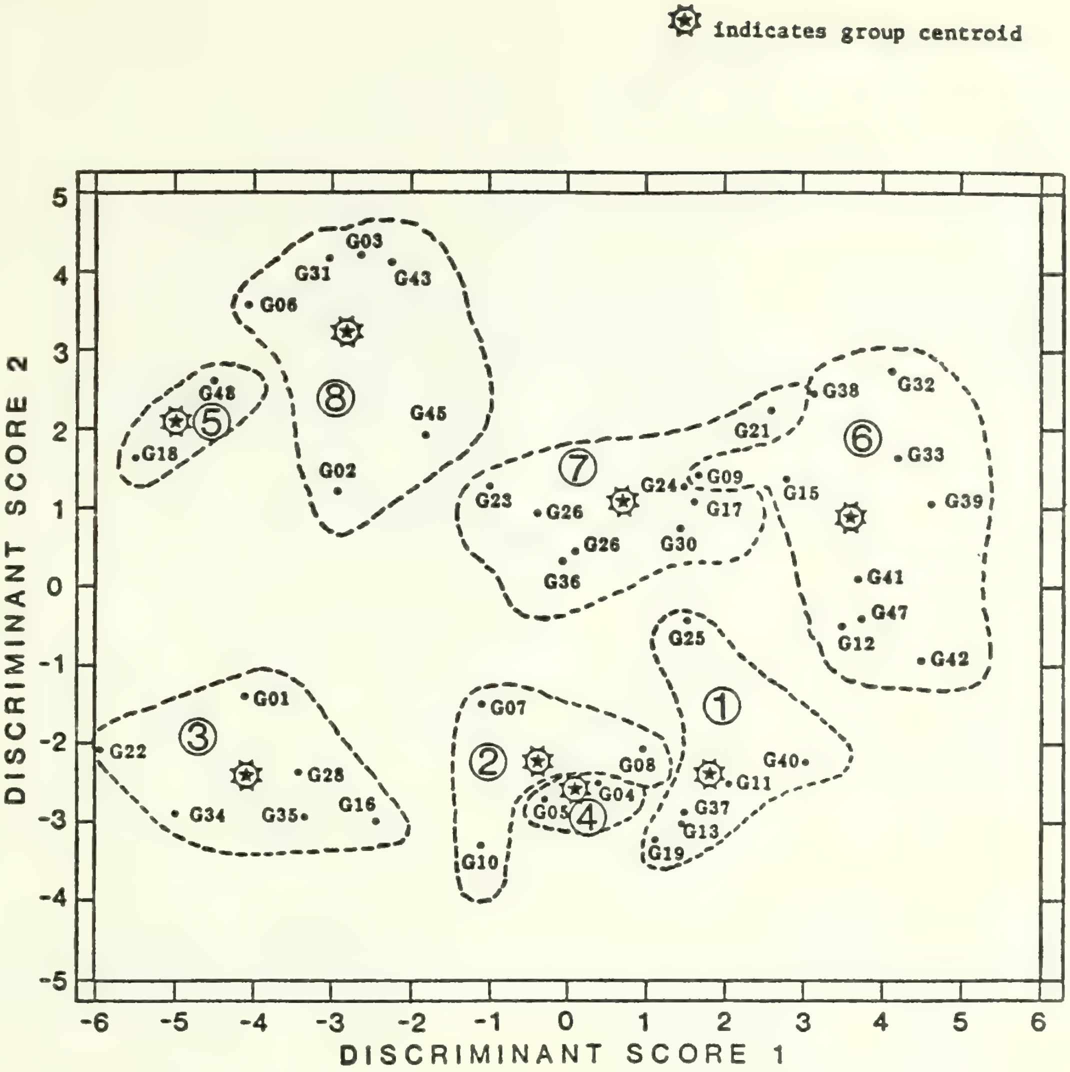


Figure 4.--Spatial relationships of bird communities on 43 of the 1977 sites when plotted using 2 discriminant functions.

provides the wildlife manager with important information. The ordination graphically portrays the degree of community "distinctness." The greater the distance between the centers of each cluster, the larger the difference in species composition.

By examining the relative abundance of the species associations within the bird community we can also generate information regarding the relative "distinctness" of the communities. The alder bird community, for example, is unique in it's abundance of species belonging to the gray catbird/swamp sparrow species association. In addition, we can see that members of this association have a narrower tolerance of different habitats than members of the mourning warbler/chestnut-sided warbler association. As with any model of a natural system, the larger the number of sample stands that are included in the original data base, the stronger are the predictions that the model can make.

Advantages

1. The approach recognizes avian communities on the basis of avian attributes rather than forcing avian community boundaries into the boundaries of vegetation communities. It thereby demonstrates similarities among avian communities that may not be intuitively obvious from a vegetation analysis alone.

Table 5. -- Species composition of the 9 major bird species associations in northeastern Minnesota.[1]

I. Mourning Warbler/Chestnut-sided Warbler	II. Red-eyed Vireo/Ovenbird	III. Common Flicker/Brown-headed Cowbird
Blue Jay Robin Cedar Waxwing Black-and-white Warbler Nashville Warbler Magnolia Warbler Chestnut-sided Warbler Mourning Warbler	Yellow-bellied Sapsucker Least Flycatcher Red-eyed Vireo Ovenbird Canada Warbler Rose-breasted Grosbeak	Common Flicker Great Crested Flycatcher Alder Flycatcher Tree Swallow Golden-winged Warbler Brown-headed Cowbird
IV. Black-capped Chickadee/Golden-crowned Kinglet	V. Gray Catbird/Swamp Sparrow	VI. Yellow-bellied Flycatcher/Connecticut Warbler
Spruce Black-capped Chickadee Brown Creeper Golden-crowned Kinglet	Killdeer Ruby-throated Hummingbird Gray Catbird Red-winged Blackbird Swamp Sparrow	Gray Jay Yellow-bellied Flycatcher Winter Wren Ruby-crowned Kinglet Cape May Warbler Connecticut Warbler
VII. Sparrow Hawk/Brown Thrasher	VIII. Hermit Thrush/Blackburian Warbler	IX. Eastern Wood Pewee/Scarlet Tanager
Sparrow Hawk Brown Trasher Brewer's Blackbird Lincoln's Sparrow	Hermit Thrush Solitary Vireo Yellow-rumped Warbler Blackburnian Warbler Evening Grosbeak Dark-eyed Junco Chipping Sparrow	Eastern Wood Pewee Red-breasted Nuthatch Black-throated Green Warbler Scarlet Tanager American Goldfinch

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[1] The strength of the relationships among the species in each association is dependent upon: 1) the amount of information available for each species and 2) the range of habitat tolerance for each species. The weaker associations in the above table include associations IV, VII and IX; all represent species that were relatively uncommon.

2. Because the boundaries of vegetation and avian communities are often similar, one can predict the relative importance of various structural features of the vegetation upon the composition of avian communities.

3. The species composition of bird communities are characterized by the relative importance of different species associations. Each species association is composed of species with similar habitat distributions.

4. Discriminant analysis allows the wildlife manager to graphically perceive the degree of faunal distinctness among the bird communities.

Disadvantages

1. Although broad vegetational requirements of a species are defined, information regarding specific niche dimensions are lacking. Data of this form are necessary prerequisites to species-oriented habitat management.

2. The technique has not been widely applied.

3. Some subjective judgements are still involved in the classification of communities and associations.

4. As was indicated in Table 5, the strength of the classification, for species associations or communities, depends on the amount of data available. For example, the strength of a species association that includes several uncommon or rare species may be less

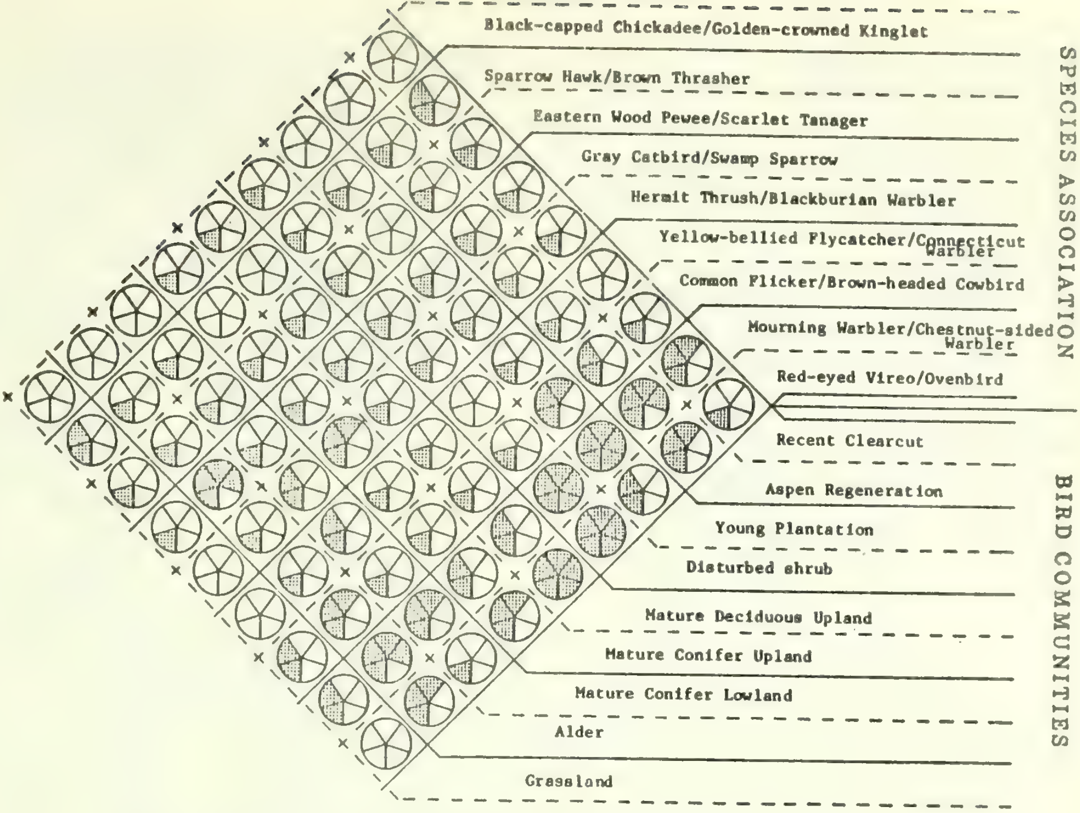
Black-capped Chickadee/Golden-crowned Kinglet
Sparrow Hawk/Brown Thrasher
Eastern Wood Pewee/Scarlet Tanager
Gray Catbird/Swamp Sparrow
Hermit Thrush/Blackburian Warbler
Yellow-bellied Flycatcher/Connecticut Warbler
Common Flicker/Brown-headed Cowbird
Mourning Warbler/Chestnut-sided Warbler
Red-eyed Vireo/Ovenbird
SPECIES ASSOCIATION
Recent Clearcut
Aspen Regeneration
Young Plantation
Disturbed shrub
Mature Deciduous Upland
Mature Conifer Upland
Mature Conifer Lowland
Alder
Grassland
BIRD COMMUNITIES

Figure 5.--The relative abundance of major species associations within bird communities of northeastern Minnesota.

(i.e., less stable) than an association that includes several abundant species.

HABITAT NICHE ANALYSIS

Background

Like the previous approach, this technique is a multivariate approach that relates habitat variables to bird distributions. Most naturalist's have recognized for a long time that certain birds occur in particular environments (Adams 1908). Some species may respond to one particular factor while others may respond to a combination of factors, thereby illustrating the need for multivariate techniques. The multivariate approach to habitat selection, and more specifically to the niche concept, was formalized by Hutchinson (1965). Hutchinson viewed the niche as an n-dimensional Euclidean space with each axis of the space corresponding to some relevant variable in the species biology. This approach has been used by Shugart and Patten (1972), Anderson and Shugart (1974), Shugart et al. (1975), Whitmore (1975), and Noon and Able (1978).

The basic premise of the approach assumes that the habitat selected by birds can be measured mathematically (see Green 1971b, 1974). If we assume that it is possible to accurately measure all niche habitat components, then it is possible to mathematically predict the probability that a species will occur in a given habitat. A key to understanding this approach involves viewing the space a species occupies as a hyperellipsoid because the individual components that define the niche are intercorrelated. For example, the density of trees directly effects the density of shrubs and herbs. Such correlations between components of the habitat implies that graphically, their axes are not orthogonal (i.e., they are not independent of one another). Subsequently, to make predictions from field data, a new coordinate system must be defined such that the axes are orthogonal or independent. These new independent axes are simply linear combinations of the original data set.

For this paper we have used principal component analysis (PCA) as modified from the work of Niemi (1977). PCA is a rotation of coordinates into a sampled hyperellipsoid. The principal component coordinates are independent and explain decreasing amounts of variation in the sample data. In PCA, a series of habitat measurements (vectors) are made within an area occupied by a species. These measurements essentially quantify the amount of a given habitat variable (e.g., tree density) that appears necessary to provide suitable habitat for the species. With an appropriate number of samples, a mean vector position or "centroid" can be calculated for each sample vector. In general, for a given habitat, the closer a habitat vector is to the species centroid position, the more suitable the habitat is for the species. A probability model can be designed to predict the occurrence of a species within a given habitat. These predictions are based on measurements of the same habitat variables used to establish the specific model. Such a model may also allow interpretation of species preference both within and between habitats (Shugart et al. 1975).

Method

We will briefly explain the methodology, but a more detailed description can be found in Niemi (1977). We constructed a model based on a PCA analysis of eight measured habitat variables (Table 6) collected within the territorial boundaries of 21 bird species found in northeastern Minnesota. These bird and habitat data were collected in four different stands during June and July of 1974 and 1975. Three stands were in young altered habitats while the fourth stand was in a mature forest habitat. The three altered stands consisted of: 1) a burned, virgin jack pine stand (BVP) which was never logged but burned in 1971, 2) a burned, cut jack pine stand (BCP) which was logged and then burned in 1971, and 3) an aspen clear-cut (ACC) stand which was logged in 1973. The mature stand was a mixed balsam - birch forest (BBF) with some aspen. These habitats were selected to demonstrate the microhabitat preferences of bird species within early successional stages and to show how a principal component model can be useful to compare changes occurring in bird populations following alteration.

Data Analysis and Interpretation

The principal component model is shown in Figure 6. The figure clearly delineates a group of species to the right, that are typically associated with mature forests, and species to the left, that are typically associated with early successional stages. Table 7 shows the correlation of the original habitat variables with the principal component for proper interpretation of the axes of the model. Those species between the two groups, such as the red-eyed vireo, veery, blue jay, and least flycatcher, are typically associated with a wide variety of habitats ranging from the early successional stages to the mature forest stages. Within the species group associated with the early successional stages, there is a noticeable gradient of species preferences from the common yellowthroat on top to the hermit thrush at the lower left (Figure 6). The yellowthroat prefers the open areas in the early successional stages along with a high density of low shrubs, and a low density of saplings and trees. The hermit thrush, however, prefers areas with high tree and sapling densities. Many species are rather ubiquitous in the early successional

Table 6.--Description of 8 variables used in the principal component analysis shown in Figure 6 including mnemonic code and method.

Variable Mnemonic	Description	Method
GC	Percent ground cover divided by 10	20(+ presence or-absence readings of green vegetatio (James and Shugart 1970)
HS	High shrub density	Number of shrub stems >1m. high <2.5cm dbh/10^{-3}ac. (Ohmann 1973)
LS	Low shrub density	Number of shrub stems $>.3$m high <1m. high/4×10^{-3}ac (Ohmann 1973)
SH	Shrub height	Average of 4 readings in m./10^{-1}ac.
SLOP	Slope	Change in elevation for diameter of 10^{-1}ac. circle
SDIV	Shrub diversity	Shannon and Weaver (1963) diversity index
SAPS	Sapling density	Number of saplings 2.5-7.6cm dbh/ 10^{-1}ac.
T2	Tree density	Number of trees 15.1-22.9cm dbh/ 10^{-1}ac.

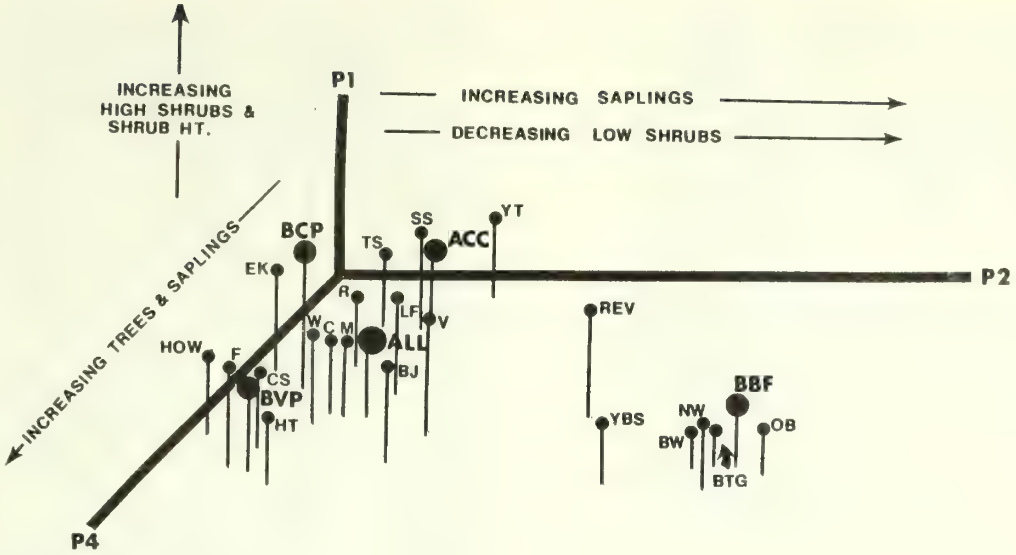

Figure 6.--Mean principal compoent vectors for twenty-one bird species and four sampled stands (described in text) on the best three principal components separating species habitat. Each axis is an orthogonal component composed of linear combinations of the eight habitat components shown in Table 7. Species include common flicker (F), yellow-bellied sapsucker (YBS), eastern kingbird (EK), least flycatcher (LF), tree swallow (TS), blue jay (BJ), house wren (HOW), American robin (R), hermit thrush (HT), veery (V), red-eyed vireo (REV), nashville warbler (NW), black-throated green warbler (BTG), blackburnian warbler (BW), chestnut-sided warbler (C), ovenbird (OB), mourning warbler (M), common yellowthroat (YT), chipping sparrow (CS), white-throated sparrow (W), and song sparrow (SS).

tages, such as the chestnut-sided warbler, ourning warbler, and white-throated sparrow; hey tend to cluster around the mean position or all (ALL) the altered habitats.

One of the interesting discoveries of his study regards an index value (Z value, able 7) that was calculated to test the elative strength of each principal compo-ent to separate the habitats selected by pecies. We found that although each prin-ipal component explained a decreasing mount of variation in the habitat data Table 7), those same components did not ecessarily explain decreasing amounts of ariation in the bird species selection of abitats. The descriptive model was con-tructed by using the best three principal omponents which separated species habitat, ot habitats alone. Birds may not differ-ntiate between habitats based simply on hose variables with high variations, but ather on variables which provide the best iscriminating cues between habitats, ariables which provide a specific need, r for other more subtle reasons. Thus, n Figure 6 and Table 7, P2, P4, and P1 ere ordered for best separating species abitats while P1, P2, and P4 were ordered n explaining variation in the habitat data.

Figure 6 provided a means to view multiple species habitat selection by multiple measurements of structural habitat components. These measurements could also include additional niche components such as food requirements, or other behavioral traits which more accurately define a species niche hyperspace. We have used principal component analysis, but discriminant function analysis may also be used to maximize the separation between species groups (James 1971; Shugart and Patten 1972; Shugart et al. 1975). Further sophistication of multivariate analysis and a more thorough testing of its field methodology will eventually provide better techniques for use in practical applications.

Advantages

1. A multivariate perspective can potentially allow a large number of species to be considered simultaneously in management objectives.
2. Presuming the assumption for collecting data are appropriate, this approach can ultimately test the strength of species associations (e.g., how closely associated are

species in a defined community) and provide a measure of the niche breadth of specific species.

3. Subjective judgements are substantially minimized relative to the approaches listed above.

Disadvantages

1. Unless an intimate understanding of both multivariate procedures and wildlife species requirements are obtained by users, these techniques may be improperly interpreted and easily abused.

2. By using the multivariate techniques, interpretation of species habitat preferences are more difficult and abstract.

3. Whether niche requirements are measurable is questionable. Presumably, there are many intangible factors which are difficult to quantify but important to the well-being of a species. See final discussion for more details.

DISCUSSION

We briefly examined four broad and diverse techniques that ecologists have implemented in their efforts to describe the relationship between animal species and their environment. We have chosen the four models presented above because they portray, in our estimation, the most realistic approaches currently available for managing many species simultaneously. A brief summary of the philosophy supporting each approach was presented, a short discussion of it's methodology, and an example of it's application. Several brief statements were also made regarding the relative merits and drawbacks of each approach. The discussion of each approach was of necessity rather general.

Giving any of the approaches justice, however, should include a detailed review of the publications cited. Hopefully our summary has provided a general review of each approach and has demonstrated that none of the techniques will provide the wildlife biologist with an all encompassing approach to species management. Since it is almost a classic response that most scientific investigations reveal far more problems than they answer, we feel it is important at this point to outline many of the problems that continually frustrate wildlife biologist who attempt to answer seemingly simple questions regarding wildlife distributions. The items listed below are drawbacks that are generally inherent to all multi-specie approaches to habitat management:

Table 7.--Z values, explained variation, and correlation coefficients of the eig habitat variables associated with t three principal components used in Figure 6. Mnemonic habitat codes a from Table 6.

	Principal Components		
Z value 1/	P2	P4	P1
Exp. Var. 2/	46.	17.	10.
Correlations 3/	21.	14.	26.
GC	.27	-.14	.39
GS	-.45	.27	.84
LS	.67	-.57	.55
SH	-.28	.27	.73
SLOP	-.02	-.20	.09
SDIV	.37	-.09	.43
SAPS	.43	.64	.29
TS	.24	.63	-.01

1/ A measure of relative strength of the principal component to separate species habitat as described in text.

2/ Variation explained by the principal component with respect to the habitat data

3/ Correlation coefficients of the principal components with the original habitat variables.

1. The delineation of communities, eithe plant or animal, is questionable. Al but one of the models described abov incorporated a subjective judgement regarding community boundaries. It i sufficient to note that some form of classification is necessary only fro the perspective of human communicati but any static classification seems useless.

4. Habitat selection by birds may be pa tially controlled by factors beyond those that can be measured within an individual's territory or home range. The size of a habitat (Whitcomb 1977; Diamond 1975) and it's spatial relationship to other habitats (Leopold 1932, Wiens 1975) are factors which

have received little attention from avian ecologists. Such factors, however, may be important components in the habitat selection process. For example, what size should clearcuts be to maintain natural populations and how should they be juxtapositioned with other habitats to benefit wildlife or a particular species?

3. Generalized approaches to wildlife management, such as those presented above, often do not take into account special habitat requirements of some species. Such democratic techniques, which manage for the "majority," may be extremely detrimental to species with specific requirements. Snags, the unmeasured variable described by Balda (1975), is an example of a neglected yet important habitat requirement for many birds. DeGraaf (1978) recently estimated that among the 800 bird species found in the United States approximately 85 are cavity nesters. For many species such as these, the absence of a single feature in the habitat could critically reduce population levels. It is crucial that potential 'limiting factors' be identified.

4. Wiens (1977) has recently summarized a concept called "ecological crunch" whereby species experience population fluctuations in response to changing environmental conditions. During times of resource limitation or stress (e.g., during drought), species may become restricted to their optimum habitats-habitats where their behavioral and morphological adaptations are best suited for securing resources. In response to these limitations, population levels may be greatly reduced. During resource abundance, however, species diffuse into submarginal habitats and, consequently, their population levels increase. This emphasizes the importance of long term studies of species populations - studies which, to date, have been seriously lacking.

5. The factors that limit population levels are poorly understood. Although most bird population studies have been conducted during the breeding season, there is a growing concern that events on the wintering grounds may be the most important factors influencing bird populations (Lack 1971), Fretwell 1973). Once again long term investigations that cover the entire life history of the species, from it's breeding grounds, to migration resting areas, and finally to wintering grounds, have been neglected.

6. A realistic approach to wildlife management must establish a means to limit the species under consideration in order to be workable. Although we have attempted such a procedure here, an important question remains - how can a wildlife manager objectively (not subjectively, as we have) decide which species to include in his management plan? The federal endangered species list, state threatened or endangered species lists, and the American Birds Blue List provide some direction for identifying species of concern. Nevertheless, these lists are also subject to individual bias and are rarely substantiated by systematic field investigations. The entire concept of "uniqueness" has escaped a much needed quantitative definition. Uniqueness criteria are difficult to define and an evaluation does not exist. Should species uniqueness be determined by niche breadth, distribution, public opinion, importance to man, importance to the ecosystem, or some other criterion? Environmental evaluations using birds and habitats, such as that presented by Graber and Graber (1976), have been progressive in this regard and deserve further attention.

7. Many ecological concepts have not been included in the models discussed above. Included among these concepts are predator-prey relationships, competition, and diversity. Until their importance is fully understood, any approach to wildlife management will, of necessity, be "simplistic" in nature.

In listing these drawbacks we do not wish to frighten wildlife biologists who endeavor to implement management approaches such as the ones we have presented here. By their very nature, all models are beset with limitations. Their objectives are to simplify natural systems, to identify the major components of the system, and to determine the species ultimate dependence upon one another, Nevertheless, we are better prepared to employ the practical applications of such models when we understand their inherent limitations.

The four approaches to non-game bird management that we have presented will serve as a framework to be expanded as our data base grows. At present we need to continue research efforts that are designed to identify species habitat requirements. Nevertheless, we have reached a starting point for wildlife impact analysis. Although we are still far from the point where the impacts of all habitat management problems can be accurately predicted, non-game bird managers can predict gross population changes based on the data we have presented.

All four management models have also been effective methods of data reduction. Beginning with an extensive list of variables that quantify the environment, principal component analysis has, after linearly combining the variables, identified those that are best able to define the response of different species in the community to environmental parameters. Features of the habitat are thereby reduced to a few 'components' that are important in the species distributions. The successional stage, life form, and species association models have, by different techniques, identified various assemblages of species. The assemblages include species which by various methods, are recognized as responding to the environment in a similar manner. As a result, the biologist can deal with groups of species rather than individual species. Work at effective methods of data reduction must continue if non-game biologists are to effectively communicate pertinent information to foresters which will aid them in understanding the implications of various habitat management alternatives.

CONCLUDING REMARKS

There are many approaches to wildlife management. The four we have examined are attempts to construct models that will simultaneously examine many species. Although the successional stage and life form approaches establish an important data base for each species, when the habitat requirements of hundreds of vertebrate species is considered, the problems are nearly incomprehensive. Thus, if managers realistically want to consider all vertebrates in the planning process, the necessity for using some form of multivariate analysis is essential. Such analyses are useless, however, unless they can be comprehended by the ecologist and wildlife manager alike. Bridging the gap between theoretical and applied ecology is not an easy task and may prove to be one of our most challenging tasks. The manager who attempts to put ecologist's models to practical use must be able to perceive how generalizations derived from the model relate to the real system he manages. In time, it would be beneficial for either theoretical ecologists to attempt interpretations of their data for practical use or a concerted effort be made to integrate theoretical findings into practical management approaches.

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THE IMPORTANCE OF WETLANDS IN THE NORTH CENTRAL AND NORTHEAST UNITED STATES TO NON-GAME BIRDS

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Abstract.--Over 200 migratory and year-round resident bird species use the diverse but limited wetland areas of the northeast and north central United States for part or all of their life requirements. Non-game and minor game (rails, coots) bird use is discussed by wetland type for both regions. Problems and causes of wetland and water bird decline are discussed; and managment recommendations for wetlands and forest managers are set forth.

INTRODUCTION

Wetland areas of the north central and northeast regions of the United States offer diverse habitats of great importance to many wildlife species, including over 200 migratory and year-round resident bird species. Nesting and feeding are the primary uses, but cover, resting, and breeding/staging uses are important. Most of these species are non-game, and have not been as intensively studied as game bird species. Over the years, however, numerous books and papers have been written in which non-game bird use of wetlands in the northern states was noted (Adams _et_ _al_. 1973; Anderson 1978; Anderson and Hamerstrom 1967; Audubon 1844a and 1844b; Beecher 1942; Bent 1921 and 1926; Berger 1951; Bergman _et_ _al_. 1970; Burger 1974; Burger 1977a and 1977b; Custer and Osborn 1977; Downing 1975; Golet and Larson 1974; Gromme 1963; Hardy 1957; Harris and Matteson 1975; Hill 1965; Johnson 1977; Kadlec and Drury 1968; Landin 1978a, 1978b, and 1978c; Martin _et_ _al_. 1951; Moseley 1936; Nicklaus 1977; Palmer 1962; Partch 1972 and 1975; Scharf 1977; Shaw and Fredine 1956; Soots and Landin 1978; Thompson 1977; Thompson and Landin 1978; Weller and Spatcher 1965; and many others). These papers tend to emphasize large water and marsh birds rather than the many smaller passerine species that also use wetlands. Some of the more informative papers which mention non-game bird use in the northern United States have been environmental impact statements prepared for or by the Corps of Engineers for various reaches of the Mississippi River system, the Great Lakes, and other parts of the northern states (Miller and Krumm 1973; Nordstrom _et_ _al_. 1974; River Studies Center 1975; Terpening _et_ _al_. 1975; U. S. Army Engineer District St. Louis 1975; and U. S. Army Engineer District St. Paul 1974) and by the U. S. Energy Research and Development Administration (Wallace 1977).

The wetlands of these two regions are as varied as the avian wildlife that use them (Shaw and Fredine 1956). Such a large area, covering 19 states from Minnesota to the north Atlantic coast and from the Great Lakes to Chesapeake Bay and the mid-Mississippi River, can only be discussed by the use of generalities. The regions have within them a number of distinct wetland types which are discussed later in this paper.

Historically, the wetland areas of both regions were much more extensive than the present day wetlands (Niering 1966). The northeastern salt marshes have been altered greatly since the early 1700s, and the interior Great Lakes marshes, fresh water swamps, and river systems have faired little better. The only areas that resemble their former expanses are the prairie pothole areas of the north central states (Stewart and Kantrud 1971), which is largely due to the intense and active interest shown in these areas by waterfowl hunters. Shipping, urbanization, recreation, flood-control, and agricultural uses are responsible in most cases for these wetland losses (Shaw and Fredine 1956). Shaw and Fredine (1956) reported only 750,834 hectares remaining in all wetland types in the northeastern states and only 4,627,820 hectares remaining in the north central states in 1956. Wetland losses have continued to occur since that time at a slower pace (Conservation Foundation 1978), but is still taking place. Wetland hectares will continue to be nibbled away because they are owned by private citizens, are not protected in all areas, and are in fringe areas which will cause them to be destroyed through changes in the surrounding environment in spite of efforts by many concerned groups to protect and manage the remaining wetlands.

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WETLAND TYPES

Shaw and Fredine (1956) described a wetland classification system that has now been outdated by the new operational draft U. S. Fish and Wildlife Service classification system of 1978 (Cowardin et al. 1977). Golet and Larson (1974) classified northeastern interior wetlands and Stewart and Kantrud (1971) did the same for the prairie pothole wetlands. For purposes of discussing bird use of these wetlands, a modification based on Shaw and Fredine (1956), Golet and Larson (1974), and Stewart and Kantrud (1971) has been devised and is used throughout this paper. Under this system, there are ten wetland types in the northeast and north central United States that are used by non-game and minor game birds during some phase of their life cycle: feeding, resting, nesting, breeding or staging, and migration.

Open Fresh Water

This wetland type is permanent fresh water 1.0-3.0 meters deep, such as ponds, lakes, rivers, and streams. It is almost always associated with other wetland types. Non-rooted aquatic macrophytes such as pondweeds (Potomogeton spp.), coontail (Ceratophyllum demersum), fanwort (Cabomba caroliniana), and other fresh water submergents, as well as duckweeds (Lemna spp.) in stillwater areas, are the usual plant species encountered in these habitats. They are used by migrating waterfowl, loons, grebes, cormorants, and coots for feeding and resting (Thompson and Landin 1978; Golet and Larson 1974). They are also used as feeding areas by fish-eating raptors, gulls, and terns (Ludwig 1968).

Deep Fresh Marsh

Permanent water areas 0.2-1.0 meters deep in areas of low energy that allow establishment of rooted aquatic plants characterizes this wetland type. This type frequently borders open water, and supports the above listed species as well as floating-leaved plants such as white water lily (Nymphaea odorata), watershield (Brasenia schreberi), and water smartweed (Polygonum amphibium). A few emergents such as cattails (Typha spp.) will occur in the shallower areas.

In addition to being the most valuable habitat for waterfowl, this type is very important to many species such as loons, grebes, and coots. It is also frequented by feeding bitterns, herons, and egrets in its shallower spots and dense floating mats. Franklin's gulls (Larus pipixcan), Forster's terns (Sterna forrteri), black terns (Sterna nigra), and American coots (Fulica americana) will seek these areas for nesting (Burger 1974; Thompson and Landin 1978).

When shrubs such as buttonbush (Cephalathus occidentalis) and willow (Salix spp.) occur in a deep marsh, the area is also used for nesting by red-winged blackbirds (Ageuaius phoeniceus and yellow-headed blackbirds (Xanthocephalus xanocephalus), and by small passerines for feeding and resting.

Shallow Fresh Marsh

This type of wetland is also highly valuable to waterfowl species for feeding, resting, and nesting. It is usually permanent water less than 0.2 meters deep, and is vegetated with cattails, wild rice (Zizania aquatica), bulrushes (Scirpus spp.), some sedges (Carex spp.), water willow (Decodon verticillatus), common reed (Phragmites australis), and other robust emergents (Golet and Larson 1974; Environmental Laboratory 1978). Shallow marshes are very important as nesting and feeding areas for red-winged blackbirds, yellow-headed blackbirds, swamp sparrows (Melospiza georgiana), and other passerines (Martin et al. 1951); for minor game water birds: common gallinules (Gallinula chloropus), soras (Parzana carolina), Virginia rails (Rallus limicola), king rails (Rallus elegans), American coots, and common snipes (Capella galinago); spotted sandpipers (Artitis macularis); and for all of the heron, egret, and bittern species (Hoffman 1978) which occur in the north central and northeast regions. Protected shallow marshes are also used by Forster's terns, black terns, common terns (Sterna hirundo), herring gulls (Larus argentatus), and ring-billed gulls (Larus delewarensis) for nesting if sufficient large vegetation is available for nest substrate and material (Burger 1974; Scharf et al. 1978).

Shallow marshes will frequently have some shrubs, usually buttonbush and willow. These shrubs, if not too dense, enhance wildlife value by increasing habitat diversity in the marsh.

Seasonally Flooded Flats

Bottomland and floodplain areas which flood more than 12 centimeters deep, usually in late fall, winter, and spring, are characteristic of this wetland type. In the summer there is little or no standing water. In this wetland type, a herbaceous cover of smartweeds (Polygonum spp.), sedges, and nutsedges (Cyperus spp.) abounds during the growing season, as well as cattails, soft rush (Juncus effusus), reed canary grass (Phalaris arundinacea), and loosestrife (Lythrum spp.). These plant communities are used by waterfowl and other ground nesting marsh birds for nesting. If a seasonally flood-wetland becomes wooded (a shrub flat or bottomland hardwood), it will become useful to tree and shrub nesting species such as colonial waterbirds and many passerines. Climax trees in such a forest include American elm (*Ulmus americana*), silver maple (*Acer saccharinum*), swamp white oak (*Quercus bicolor*), pin oak (*Quercus palustris*), eastern cottonwood (*Populus deltoides*), and others. Intermediate plant species include willows, dogwoods (*Cornus* spp.) buttonbush, meadow-sweet (*Spiraea latifolia*), and red maple (*Acer rubrum*).

The presence of several life forms in this type of wetland increases its value, and many passerines such as yellowthroats (*Geothlypis trichas*), song sparrows (*Melospiza melodia*), swamp sparrows, yellow warblers (*Dendroica petechia*), and eastern kingbirds (*Tyrannus tyrannus*) nest there (Golet and Larson 1974). Such areas are also used extensively by and are important to migrating waterfowl and other marsh and water birds (in the southern United States, this wetland type is one of the most important, as it accomodates many thousands of overwintering waterfowl and other species).

Wet Meadows

This wetland type is seasonally flooded to less than 12 centimeters deep. Reed canary grass, blue joint grass (*Calamagrostis canadensis*), many species of sedges and nutsedges, boneset (*Eupatorium perfoliatum*), and Joe-pye weed (*Eupatorium* sp.) are common components of these communities. Composition of plant species, and therefore wildlife value, is strongly influenced by grazing. A heavily grazed meadow tends to consist almost entirely of soft rush, as cattle will not eat it. Wet meadows are used by several species of passerines for feeding, especially flocks of robins (*Turdus migratorius*), cowbirds (*Molothrus ater*), starlings (*Sturnus vulgaris*), grackles (*Quiscalus quiscala*), blackbirds, and sparrows (Martin *et al.* 1951); red-winged and yellow-headed blackbirds and song and swamp sparrows will nest there.

Shrub Swamp

Permanently flooded areas with shrub stands consisting of buttonbush, red maple, willows, silky dogwood (*Cornus amomum*), gray dogwood (*Cornus racemosa*), red-osier dogwood (*Cornus stolonifera*), highbush blueberry (*Vaccinium corymbosum*), viburnums (*Viburnum* spp.). and sweet-gale (*Myrica gale*) characterize this wetland type. Nesting passerines are the primary users of shrub swamp, but its value varies with the plant species composition and plant community structure.

Wooded Swamp

This wetland type is primarily hardwoods in river and stream floodplains which are seasonally flooded up to 1 meter deep. It also includes wooded areas which are permanently flooded, but these primarily occur in the southern United States and are characterized by bald cypress (*Taxodium distichum*) and Tupelo gum (*Nyssa sylvatica*). The wooded swamps of the north are largely composed of silver maple, swamp white oak, pin oak, green ash (*Fraxinus pennsylvanica*), American elm, eastern cottonwood, willow, and red maple. In the more permanently flooded swamps, red maple is the dominant species. These areas are valuable as breeding habitat for not only wood ducks (*Aix sponsa*) and black ducks (*Anas rubripes*), but for many species of herons, egrets, warblers, flycatchers, woodpeckers, thrushes, nuthatches, vireos, rose-breasted grosbeaks (*Pheucticus ludovicianus*), hawks, owls, grackles, and many passerines (Golet and Larson 1974).

Coniferous wooded swamps have red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*) in highlands swamp areas, and Atlantic white cedar (*Chamaecyparis thyoides*) in the lowland swamps. These evergreen swamps provide nesting and feeding habitat for golden-crowned kinglets (*Regulus satrapa*), magnolia warblers (*Dendroica magnolia*), red-breasted nuthatches (*Sitta canadensis*), and other warblers (Golet and Larson 1974; Robbins *et al.* 1966).

Acid Bogs

Bogs are formed from deep accumulations of sphagnum moss and usually have very acid pH ranges. This acid, low oxygen environment is not conducive to good wildlife habitat. However, the bogs are used by some ducks for feeding and by warblers, flycatchers, nuthatches, and kinglets for nesting.

Characteristic vegetation of upland bogs included black spruce (*Picea mariana*), tamarack (*Larix laricina*), leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*), sweet-gale, and cranberries (*Vaccinium marcocarpon*). Lowland bogs are dominated by Atlantic white cedar with red maple and leatherleaf common.

Salt Marshes

This wetland type occurs in the north only on the Atlantic coast. It included brackish and salt marshes of all categories (deep, shallow, brackish, saline, but are all tidally influenced) occurring on the coast from Maine to Maryland. These salt marshes are dominated by smooth cordgrass (*Spartina alterniflora*) and glasswort (*Salicornia* spp.) in saline areas;

saltmeadow cordgrass (Spartina patens), saltgrass (Distichlis spicata), saltmarsh bulrush (Scirpus robustus), marsh elder (Iva frutescens) and other species in brackish marshes; and with common reed dominating fresh to slightly brackish coastal marshes (Environmental Laboratory 1978; Hunt et al. 1978).

The salt marshes are used extensively for feeding, nesting, and resting habitat by common terns, roseate terns (Sterna dougallii), great black-backed gulls (Larus marinus), herring gulls, laughing gulls (Larus articilla) (in the extreme southern parts of the northeast only), clapper rails (Rallus longirostris), black rails (Laterallus jamaicensis), all herons and egrets except cattle egrets (Bubulcus ibis) in the area, willets (Cataphrophorus semipalmatus) and glossy ibises (Plegadis falcinellus) (Burger 1977a; Robbins et al. 1966; Soots and Landin 1978). Least bittersn (Ixobrychus exilis) also inhabit brackish marshes, as do king rails (Meanley and Wetherbee 1962). Long-billed marsh wrens (Telmadytes palustris), short-billed marsh wrens (Cistothorus platensis), seaside sparrows (Ammospiza maritima), sharp-tailed sparrows (Ammospiza caudacuta) also use salt marshes for nesting, although sharp-tailed sparrows frequently only overwinter in salt marshes (Pettingill 1970; Robbins et al. 1966).

Open Salt Water

Low energy areas that allow growth of aquatics such as eelgrass (Zostera maritima) and wild celery (Vallisneria americana), and marine algae are characteristic of this wetland type. These areas are used extensively by overwintering waterfowl. They are also used heavily by overwintering coots, loons, and grebes. Open estuarine and bay waters are used extensively for feeding by royal terns (Sterna maxima), common terns, roseate terns, Caspian terns (Sterna caspia), least terns (Sterna albifrons), and herring and great black-backed gulls. These species nest on isolated high sites and islands within the wetland area, many of them on dredged material islands (Landin 1978b). The open water areas of this wetland type are generally behind barrier islands, and in bays, coves, and estuaries.

Ideal Wetlands

The ten wetland types are used in varying degrees by non-game and minor game bird species, with wooded swamps and deep and shallow permanent marsh offering the most valuable and diverse habitat. A reasonable generalization is that wetlands increase in value to wetland-using non-game and minor game birds if they:

a. Are located in bottomlands in a fairly large tract of land,
b. Are close to open water and have a stable water supply,
c. Have neutral pH and fertile soil,
d. Offer diversity of vegetation life forms,
e. Are isolated from human populations, and
f. Are free of contaminants.

A wetland is of least value if it is a small upland area with no open water nor permanent water supply, is subject to acidity from deca ing vegetation, is in poor soils, has been contaminated from either point or non-point source, and is near urban areas or areas used for recreation. These two extremes of ideal and worst case northern wetlands are of cours hypothetical, and most wetlands in the two regions lie between the extremes. The key to increasing non-game bird species use of a wetland lies with developing more of the remaining wetlands of the area into quality habitat and allowing less of it to fall toward the less valuable wetland extreme.

WATER BIRDS

While northern United States wetlands ar undoubtedly of immense importance to passerin species, those bird species that will be affected most severely by continued loss or alteration of wetlands are those groups commonly called water birds (herons, egrets, cormor ants, ibises, loons, gulls, terns, skimmers, bitterns, grebes, rails, and coots). In the northern states, these species are not abundant with the exception of the ring-billed gull in the Great Lakes and the herring gull on the northeast coast (Soots and Landin 1978).

Declines in populations of great blue herons and common egrets have been noted by Thompson (1977), Thompson and Landin (1978), and Norling (1977). The wading birds in the interior United States are often subjected to contaminated feeding areas (Konermann et al. 1978; Hoffman and Curnow 1977; Keith 1966) although the fish-eating terns and other specie seem to encounter less problems from contamination than do the wading marsh feeders. This contamination effect is especially true in the large river systems (Thompson 1977) and the Great Lakes (Hoffman and Curnow 1977). The most frequently encountered problem in th northeast with species such as herons, egrets, terns, and skimmers is human disturbance and a reduction in the quality of their feeding areas (Soots and Landin 1978; Gochfeld 1977; Buckley and Buckley 1976). However, an increase in nesting great blue herons, glossy ibises, Louisiana herons (Hydranassa tricolor), snowy egrets (Leuciphoyx thula), common egrets, cattle egrets, black-crowned night herons (Nycticorax nycticorax) has been noted in the

New England area on offshore islands (Dick Forster, 1979, Massachusetts Audubon Society, personal communication. Forster also reported that common and roseate terns there are declining. Possible causes are similar to problems elsewhere; habitat loss, decline in water quality, and human disturbance.

The least tern is dwindling in numbers on the coasts, and the interior least tern has all but disappeared from its former nesting areas in the Mississippi River and its tributaries (Downing 1975; Hardy 1957). In the rivers, the loss is due to the lack of undisturbed sand bars suitable for nesting (Thompson and Landin 1978), and on the coast it is due almost entirely to lack of bare sand areas and human disturbance and its ramifications (pets roaming through colonies, motorcycle enthusiasts, campers, curious people wanting to "look at the bird eggs and the baby birds", and similar events] (Soots and Landin 1978. The need for bare undisturbed nesting areas is great throughout the least tern's range

Other tern species are either declining in population or are stable, but none are increasing even though Forster's tern has recently extended its range into the Mississippi River (Thompson and Landin 1978). Common terns that have difficulty successfully nesting in the Great Lakes are bothered by night heron, herring gull, and ring-billed gull predation, and lack of suitable nesting habitat. Common terns on the coast have become largely salt marsh nesters (Burger and Lesser 1977) because other suitable isolated sites do not exist (Landin 1978b).

Piping plovers (Charadrius melodus) are small shorebirds that have used upland sand areas and islands in or near Lake Superior wetlands for nesting; their numbers have diminished dramatically in that area because nesting habitat has not remained available to them (Robert Whiting, 1978, U.S. Army Engineer District, St. Paul, personal communication).

Double-crested cormorants (Phalacrocorax auritus) are listed as endangered in Wisconsin (Wallace 1977) and are quite limited in Michigan and other areas of the north central region. The primary cause of their demise has been human persecution and loss of nesting trees, not necessarily loss of wetlands habitat. In a colony of double-crested cormorants in the Upper Mississippi River, a set of nesting boxes have been erected to replace nest trees that have fallen in an old flooded stump field.

The night herons have never been common in the northern states, especially the yellow-crowned night heron (Nyctanassa violacea), and they have decreased in numbers over a period of years with the exception of the New England area, The reasons for this decline are unclear, but it is believed that the cause is contaminated feeding areas (Ohlendorf *et al.* 1978; Bull 1964).

Bitterns are elusive and an accurate estimate is hard to obtain (Willer 1961), but Wallace (1977) believes that the American bittern (Botaurus lentiginosus) is probably declining in numbers in the Great Lakes area. The least bittern is still common throughout northeast fresh marshes, but it possibly is declining in total numbers also.

Gulls and cattle egrets are the only species that seem to be having little problem adjusting to increasing human populations and decreasing wetland habitats. This is due largely to the fact that cattle egrets are primarily upland feeders, and gulls are scavengers of human garbage which adds large new food sources to their traditional fish/scavenge diet (Soots and Landin 1978; Schrieber and Schrieber 1978).

Ludwig and Tomoff (1966) studies reproductive success in an insecticide residue environment in Lake Michigan, but these residues have had no real effect on the total population in the Great Lakes.

The common loon (Gavia immer) and, less commonly, the red-throated loon(Gavia stellata) are species occurring in the northern states Although botulism die-off has killed large numbers in the past decade (Wallace 1977), populations are still not believed to be in serious trouble. These birds, especially the common loon, overwinters in marine waters, but nests near open water in fresh marshes (Robbins *et al.* 1966). Martin (1978) has indicated that loons are declining in New England.

PROBLEMS AND CAUSES

Almost all the problems affecting water bird populations and their survival are related to human causes. Increased human populations, especially in the already highly populated northeast and north central states, causes loss or alteration of wetlands due to:

a. Increased recreational use of wetlands (boating, fishing, hunting, bird-watching (Soots and Landin 1978);
b. Drain and fill operations for agricultural and urban use which include mosquito-ditching (Burger 1977b), draining and using former wetlands for agricultural lands (Shaw and Fredine 1956), dredged material fill for marinas and waterfront properties, and other alternatives;
c. Industrial, agricultural, and human wastes in wetlands which

include placement of dredged material from shipping channels on or near wetlands, excessive nutrient loands and pesticides from farming and sewage; and heavy metals and chemicals from industry (Hunt et al. 1978); and

d. Water table and lake level changes from the drawing of fresh water from underground reservoirs for urban use, and the damming, streamlining, or deepening of lakes that cause their level of water to fluctuate.

The wetlands in the nertheast and north central United States have been greatly affected by the above activities. Because wetlands are affected, the bird species that use wetland habitats for any part of their life cycle will decline or increase as a result of changes in those wetlands. Impacts on wetlands have impacted non-game and minor game bird species in several ways. Feeding habitat has decreased or become contaminated, especially in the interior areas (Hoffman and Curnow 1977; Konermann et al. 1978; Thompson 1977; Keith 1966). Nesting site disruption is caused by cutting or clearing vegetation from shrub and wooded swamps, making colony sites accessible to human activities or destroying those colonies, removing the water by draining, and for many other reasons. Resting and loafing sites are affected for the same reasons, except that isolation is not so critical.

All birds are vulnerable while nesting (Pettingill 1970), as they must remain in one location for the duration of the breeding season. Water birds (Herons, egrets, terns, gulls, and others) will nest in large conspicuous colonies and will fly for long distances to reach a desirable feeding area from their nesting site. The herons on West Sister Island in Lake Erie often fly several kilometers to natural and manmade marshes to feed (Soots and Landin 1978).

All birds need differing amounts of seclusion for reproduction to take place (Pettingill 1970). Strongly territorial nesters require this most; i.e., the bald eagle (Haliaeetus leucocephalus) which requires large land expanses around its nest before it will successfully reproduce. Colonial nesting birds, while nesting in dense colonies, still have territorial and nest spacing requirements before they can successfully raise a brood (Soots and Landin 1978; Wiese 1977 and 1978). These birds will tolerate more interference by human colony intruders and observers than non-colonial or solitary nesters (Anderson 1978), but more damage can be done to a given population by entering a colony than in any other way (Soots and Landin 1978).

Solitary nesting birds such as bitterns, rails, and others have a great need of seclusion and thus will tolerate little or no intrusion by humans (Bent 1926; Palmer 1962).

Migratory resting points for not only waterfowl but the numerous non-game and minor game birds which migrate are necessary for many species who stop periodically along their route rather than fly non-stop. Any alternation or destruction of these wetland resting points will have an impact on the number of birds that successfully complete the migration (Scharf 1977).

MANAGEMENT RECOMMENDATIONS

The losses of wetlands over the past 200 years have been tremendous, and the damage is not likely to ever be undone, even in future generations. The wetlands that are now urban and recreational sites, farm lands, and reservoirs will undoubtedly remain as they are now. Pressures are still being placed that put existing wetlands in question, in spite of the Clean Water Act and its Section 404 regulations.

It should be noted that, realistically speaking, a wetlands manager cannot expect to expand the wetlands outside the land he can control, whether it is refuges, game farms, game management areas, or commercial forest operations. In spite of these limitations, even a modest impact by that manager would be of benefit when it was grouped with efforts throughout the region for the benefit of wetlands as wildlife habitat.

Broad Recommendations

There are several obvious recommendations for wetlands that can be made to all wetlands managers and people concerned with the continued existence of wetland areas. First, all the remaining wetlands in the northeast and north central United States should be maintained and enhanced where possible for the benefit of non-game as well as game species. A great deal of emphasis is still placed only on game bird species that use wetlands. Fortunately for the non-game birds, management of areas for waterfowl has helped preserve some habitat for them as well.

Second, the possibility of converting some lands under federal, state, or public ownership back to wetlands from their present status should be investigated, and where it is possible to create quality habitat by this method, it should be done. There are marginal lands in public ownership that could be managed to bring them up to quality habitat by such methods as planting suitable vegetation (Environmental Laboratory 1978); by changing the water level using low-head dams or dikes; and by posting or fencing them to prevent human intrusion (Soots and Landin 1978).

A third broad recommendation is for agencies to continue to do as they have recently begun, and continue to seek and acquire blocks of land from private owners that can be preserved or returned to wetland habitat. These lands are usually under the control of the state conservation agencies, and can be managed to increase their wildlife value. One of the drawbacks in the U. S. Fish and Wildlife Service's acquisition program has been such problems as state agencies not having the funds and the personnel to manage these blocks of land that have come under their control. Another drawback in the same program has been emphasis on mangement for waterfowl only, with not much regard for the non-game birds that would use these areas. In spite of these problems, the program is well worth continuing.

A study that is beginning at the U. S. Army Engineer Waterways Experiment Station which may aid managers in taking marginal poor quality lands and developing and managing them to become higher quality habitat should aid in mitigation efforts of wildlife habitat to be displaced by Corps activities. The research station is also continuing research begun under the auspices of the Dredged Material Research Program (DMRP) on habitat development and management of land areas created from dredged material.

Specific Recommendations

Most specific recommendations can be directed to forest managers who have wetland areas within their control. Close examination of all wetland areas in control and determination of their use and quality could be based on the criteria perviously discussed. If there is quality habitat within an area, it should be maintained and stabilized as it then exists.

Since acid, non-fertile areas are not conducive to wildlife use, these areas could be changed possibly by raising the pH and fertility levels of the wetland, as has been done in areas of the south. This should be approached carefully, however, as this recommendation would also apply to acid bogs, and these areas are often unique. They usually have plant species found in few other places, and any unusual plants should not be disturbed if it is determined that they are in fact rare or endangered.

Building low-head dams or dikes to allow intermittent ponds to become shallow marshes and ponds and to control water levels is another fairly simple way to increase the habitat value. This has already been done in many areas of the northeast and in the southern states (Landin 1978a).

In large open areas where wave action causes erosion problems and prevents much wildlife use, erection of wave barriers or dikes may be necessary to allow marsh formation and to create stillwater areas for feeding birds (Environmental Laboratory 1978). This has been done during the creation of a large new disposal site by the U. S. Army Engineer District, Detroit, in which they deliberately built the disposal dike in an area where a natural marsh would be protected and its eroded parts allowed to rebuild. The area will provide feeding habitat for water birds both behind the site in the existing marsh and inside the dike after it is competed (Richard Gutleber, 1978, U. S. Army Engineer District, Detroit, personal communication). An inovative wave barrier built of floating tire breakwaters in marine areas is being tested in research at the University of Rhode Island.

A fairly inexpensive way to increase the wetland's value is to plant suitable plant species that will be of value to target wildlife species as feeding, resting, and/or nesting habitat (Hunt et al. 1978; Environmental Laboratory 1978). If too many plants are there, as in the case of a thick shrub swamp, shallow marsh, or overgrown bird colony site that has been overtaken by undesirable or an excess of plants, a thinning of these plants to bring back open areas and a diversity in habitat would be of benefit (Soots and Landin 1978).

Precedents for providing nesting areas for birds, such as nesting platforms for ospreys (Pandion haliaetus) in New Jersey and open nesting boxes for cormorants in the Upper Mississippi River (Thompson and Landin 1978), have already been made. In areas of diminishing nesting habitat where birds will not move but slowly decrease in population, this action may be necessary. This may also be the case where an all-out effort to bring back a species, such as the osprey program in New Jersey, needs to be made (Joan Galli, 1976, New Jersey Nongame Biologist, Trenton, personal communication).

One of the most critical needs for non-game bird management is the creation of seclusion and isolation from humans by fencing, posting, law enforcement, or whatever other actions are necessary to insure that colonies and sensitive nesters are undisturbed (Soots and Landin 1978; Buckley and Buckley 1976). Those non-game birds that need this effort most critically are all species of terns, especially the least tern; the herons and egrets of the Great Lakes and interior areas; and the cormorants in the river systems and Great Lakes. These birds are all declining in population. Provision of undisturbed nesting sites which are lacking at the present time for least terns, common terns, roseate terns, and black skimmers (*Rynchops nigra*) needs to be made. One of the determinations of best use of dredged material by the DMRP has been the placement of fresh dredged material on Corps and other islands for the use of these nesters. The main drawback to this placement has been and probably will continue to be the immediate use by humans of these new sand areas for recreational purposes, especially in the river systems (Richard Baker, 1977, U. S. Army Engineer District, Rock Island, personal communication), which does not give the birds a chance to nest.

Another practice that is recommended and can be implemented by forest managers is leaving vegetation on stream banks, lakesides, and marshes; clearcutting of these areas removes the cover that had been present for many bird species. Numerous passerines nest in the edge of wooded areas adjacent to open water. Wading birds use these areas as cover while hunting for food, and they depend upon the clarity of the water to see their prey. Cutting of streambanks has been shown to greatly increase the muddiness of the water. The recommendation that a 15-20 meter deep fringe to streams, lakes, rivers, and marshes be left would allow critical habitat to remain and protection of the water quality (Russell 1966).

Water levels can be raised or lowered to manipulate vegetation to increase non-game bird habitat. The provision of open water in a marsh area or wooded swamp allows feeding areas for not only waterfowl and the species previously discussed, but allows belted kingfishers (*Megaceryle alcyon*) and above-water feeding swallows and martins feeding habitat not otherwise provided.

SUMMARY

Wetlands as they existed when this country was settled will never be regained; however, there is much that can be done to not only save that which is left but to enhance its value to wildlife. A continuing and dedicated effort to protect and manage existing wetlands; acquire any new wetland or potential wetland areas for preservation; increase the quality of wildlife habitat, especially for non-game species; and to prevent increasing human populations from intruding into wildlife areas, especially during the critical nesting season, to the detriment of that wildlife must be made by all wetlands and forest managers everwhere. The concern of all persons and responsible agencies is vital to the continuation of the wildlife species which depend upon wetlands for their life requirements. Only when everyone works together will these efforts be successful.

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BIRDS OF UPLAND OPENINGS

Charlotte M. Taylor and William E. Taylor[1/]

Abstract.--Northern forest openings are variable in vegetative life form. Eighty species of nongame birds are associated with forest openings or edge of forest openings in Northern Michigan. Current management is reviewed and suggestions for additional management practices and studies are included.

INTRODUCTION

Upland openings are an integral part of the forest environment. They are the beginning stage in the development of a forest and differ greatly from the usual mental image of a forest represented by trees. Their physical aspect is very different and their biological production - plants and animals - is very different from that of a stand of timber.

Management of forest upland openings is a controversial subject. To the wildlife biologist they represent a unique vegetative association which produces animals not produced in any other vegetative association of the forest. The timber manager looks at upland openings as nonproducing forest lands. This may be a logical consequence since the production of an acre of timber has an identified value while the production of a forest opening is incompletely documented (documented only in terms of a few known game species).

This discussion will review some of the existing information about upland forest openings and attempt to emphasize the value of this vegetative type to nongame birds.

Included are a description of upland openings, a listing of the nongame birds found associated with them, a review of current management, and recommendations for additional management consideration.

Upland openings come in a variety of sizes, shapes, and vegetative forms. All are important when discussing bird communities.

Large upland openings are generally referred to as fields, pastures, abandoned pastures, cultivated areas, grasslands, and/or prairies. Small openings are referred to as forest openings; they may be grassy openings or, if with shrubs and trees, brushy openings.

The importance of upland openings is recognized generally in terms of their importance to game species. McCaffery and Creed (1969) demonstrated the importance of upland forest openings to deer. They consider that "... the principal value of openings to all forms of forest wildlife lies in the variety of vegetation they provide." They acknowledge that "... these values are inadequately known in a quantative sense," but some are at least qualitatively recognized.

Dr. Peterle (1954) and Dr. Amman (1957) documented the necessity of maintaining wildland openings - 640 acres (260 hectares) and larger - if sharptail grouse are to continue as a species in Michigan. Robert Dorney (1959) described the importance of upland openings for ruffed grouse in Wisconsin.

Most studies dealing with nongame birds of upland openings are with large grasslands, cultivated areas, or nonforest types.

Watkins (1895), Frothingham (1900), and Blackwelder (1909) described breeding birds (and others) found in various large open types in Michigan about the turn of the century - about the time of major conversion from forest to farm - and from trees to ashes. More recent work by Kendeigh (1948) in the northern part of the Lower Peninsula of Michigan includes a brief account of breeding birds of a large (100 acre or 40 hectares) meadow.

Breeding bird censuses, American Birds (1973-1978), include studies of fields,

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cultivated areas, and various forest types. Since the minimum size for such studies is twenty-five acres, small forest openings are not included. If clearcutting fits the definition of upland opening, then studies dealing with recently clearcut forest types (Niemi, 1974) provide information about breeding birds in forest openings.

In another study in Minnesota, Barbara Bergstedt and G. Niemi (1974) compared breeding bird populations inhabitating a recent burned and unburned forest. Depending upon the physical structures or life form remaining after the fire, and again depending on the definition of upland opening, the burned forest may be an upland opening.

Dr. Gysel's study of the vegetation and animal use of a powerline right-of-way in Southern Michigan (1962) was one of the first to specifically consider small forest openings and nongame birds. Herman Shugart and D. James (1973) bridged the gap between field and early forest stages in the Study of Ecological Succession of Breeding Bird Populations in Northwestern Arkansas.

It is difficult to make regional interpretations of local bird population studies, or to make local interpretations of regional studies for several reasons. The same bird species may occur in totally different ecological types (deciduous versus conifer type) in different parts of its breeding range, (Kendeigh, 1945). The lack of standardization of type description currently in use makes it difficult at best, and frequently impossible, to interpret or compile summaries (Shugart and James, 1973). This difficulty is compounded by considerable natural variation within the same type. G. Niemi recognized difficulties in measuring changes (comparing populations) of breeding bird populations due in part to lack of homogeneity, or great heterogeneity of habitats, especially where small forest openings are concerned (Niemi, undated). Opening size and the size of the surrounding vegetative type have an important influence on the species component of inhabitating communities (Bond, 1957) but, except for birds like sharptail grouse or upland sandpiper, the relationship is poorly understood.

The description of vegetative types does not always recognize important habitat components. L. Brecker, (1943) recognized life form, "...the physical aspect of the vegetation or the materials in, on, or from which the bird builds its nest, seeks its food and finds its shelter," as a very important factor governing the suitability or availability of the niche. F. James (1971) and H. Shugart and B. Patten (1972) identified and demonstrated life form or vegetative stru ture as a determinant factor in the selectio of niche by birds, yet few if any existing studies use vegetative type descriptions whi consider life form in any but the most gener way. For instance, a description of a pole size hardwood stand does not include information about understory or ground vegetation.

DESCRIPTION OF UPLAND FOREST OPENINGS

Upland openings are different things to different land managers. To a forester an upland opening is an area with 10% stocking of commercial forest trees and with grass. An opening with 16% or less stocking of seedling and saplings (less than 5" dbh) is considered as a nonstocked stand. A stand is defined as an area of uniform vegetation composition and structure. Forest biologists generally recognize upland openings as any area without tree There are grassy openings, grass and forb ope ings, and shrub openings. The shrubs may be young trees. A nonstocked stand may be consi ered an opening or it may be considered a sparse stand of trees.

Openings are vegetative stages in the su cession pattern of the forest. Their life sp - how long they last - depends upon their veg tative composition. In Minnesota the length time since the last major disturbance and the type of vegetation present at the time of disturbance are important factors in determining the structure and composition of the present plant community (Ohmann, 1973). The formatio of dense sod contributes to the lasting qualities of upland openings. Sod openings will last 40-50 years or more if undisturbed. The age of some openings in the northern hardwood types in the Upper Peninsula of Michigan is estimated to be 50 years - Kendeigh found meadows in the northern part of the Lower Peninsula of Michigan changed very little in 29 years (Kendeigh, 1948). Similar situations exist in Minnesota (J. Mathison, 1978).[2/]

Sod development in a forest environment results from repeated burns, or intensive burns, cultivation, heavy grazing, or mechanical action which causes soil compaction or herbicide use (J. Wigger, 1978).[3/]

Size is a most obvious feature of upland openings and is perhaps one of the more important. Breeding birds found in large openings

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2/ Mathison, John, 1978, Personal Communication, U.S. Forest Service, U.S. Department of Agriculture.

3/ Wigger, Gerald, 1978, Personal Communication, U.S. Forest Service, U.S. Department of Agriculture.

are different from those associated with small openings: Watkins (1895), Blackwelder (1909), Frothingham (1906), and Kendeigh (1945, 1948). Weather conditions (microclimate) are very different in large and small openings. Forest Stearns and B. Ringger (1972) found that in large openings extremes and duration of extremes of temperature are very different than in smaller openings.

The distinction between large and small openings is difficult to make. Effective size, in terms of solar radiation, wind movement at ground level, mean and maximum temperature, and relative humidity depend upon the height of the surrounding trees. Dr. Stearns and Ms. Ringger used the ratio of opening diameter to height of surrounding trees to express opening size.

The size in acres of openings of different D/H ratios in different timber types (vegetative types) are indicated in Table 1.

Openings with a D/H ratio of 0.05:1 and smaller are no different than the surrounding forest, in terms of wind movement, solar radiation, radiation out from the opening, and relative humidity. Openings with D/H ratio of 1:1 and D/H 2:1 experience highest average maximum temperature and longest periods of high relative humidity. Wind barely penetrates into them, they have longer frost free periods, and mosquitoes and deer flies are more abundant. Large openings have a D/H ratio of 6:1 or 10:1 or more. Openings with D/H ratio of 10:1 to D/H ratio 20:1 and larger are more appropriately considered grasslands rather than forest openings. (Ringger and Stearns, 1972).

Vegetative composition (species composition) of openings appears less important than the growth form or life form - the overall shapes of the vegetation. Kendeigh (1948) and Bond (1957) recognized that community segregation of birds is correlated with types of vegetation rather than species of plants involved. Kendeigh observed the occurence of some structure: stump, snag, or post, was a suitable substitute for a particular life form plant. Because of its presence birds were invited into areas not normally occupied. S. Ulfstrand (1975) observed that in habitats containing the same number of trees and shrub species, flock diversity of birds will be higher the more structurally diversified the vegetation.

Studies by F. James (1971), H. Shugart and D. James (1973), and J. Niemi (no date), demonstrate the ability to associate bird species with life form rather than species composition.

Upland openings do not exist without edge. Edges have been considered especially productive areas for many species of birds. Studies in mixed forest type borders (edges) by Marten (1960) in Ontario, documented large populations of birds - more species were present there than were found in the interior forest. Egler (1966) considered the edge between forest and upland opening (right-of-way) to be valuable habitat for nongame birds. Gates and Gysel (1978) working in a continuous field-forest edge found that with increasing distance from the edge, changes in habitat composition and structure apparently resulted in decreasing numbers of nests of the open-nesting passerines found during their study. They also found that over half of the nests were found within 15 meters (approximately 50 feet) of the edge. Seventy-five percent of the nests belonged to birds characteristic of mixed breeding habitat, i.e., birds requiring an open vegetative canopy with dense cover near the ground for nesting and feeding, and elevated singing and observation perches.

Carlson (1976) found in an opening-jack pine mixture in Northern Michigan that all successful nests of bluebirds were in habitat that contained both open areas with scattered trees and densely stocked areas.

Although the importance of "edge" for a diversity of species has been emphasized by a number of authors, Gates and Gysel (1978) have issued a warning about the dangers inherent in narrow edge situations and question their value. They do not dispute the importance of edge; indeed in their study at Rose Lake they found most nests there, but nesting success was greatly reduced. They cited predation and cowbird parasitism as the most important reasons for failures, and believe the increased predation rate was a response to the concentration of nests. They propose that narrow man-made forest edges could well function as "ecological traps" for avian species characteristic of habitats with mixed life form. Because they say extensive areas of narrow field-forest edge have only been in existence for a brief period relative to the evolutionary time scale, these may then not be like the ecological niche in which these mixed habitat species developed and so they may not be able to cope with the increased predation. The most important aspects of upland openings are vegetative life form and size.

BIRDS OF UPLAND OPENINGS

The preparation or interpretation of a list of birds of upland openings must be done with considerable reservation. R. Bond (1957) and S.C. Kendeigh (1945, 1948) both indicate that bird populations are not really divisible

Table 1.--Acres - Size of Opening by D/H and Tree Height.

D/H Ratio	White Pine 85'	Maple 80'	Red Pine 70'	Aspen 65'	Spruce Fir 50' Jack Pine 50'
1:1	.52	.46	.35	0.30	0.18
2:1	2.08	1.85	1.41	1.22	.72
3:1	4.69	4.15	3.18	2.75	1.62
4:1	8.34	7.39	5.65	4.88	2.88
5:1	13.01	11.54	8.83	7.62	4.51
6:1	18.76	16.62	12.72	10.97	6.49
7:1	25.53	22.62	17.32	14.93	8.83
8:1	33.35	29.54	22.62	19.50	11.54
9:1	42.21	37.39	28.62	24.68	14.60
10:1	52.11	46.16	35.34	30.47	18.03
20:1	208.43	184.63	141.36	121.88	72.12
30:1	468.97	415.42	318.05	274.24	162.27
40:1	833.72	738.52	565.41	487.54	288.48
50:1	1302.69	1153.94	883.48	761.78	450.76
60:1	1875.87	1661.67	1272.22	1096.96	649.09
70:1	2553.27	2261.72	1731.63	1493.09	883.48
80:1	3334.88	2954.08	2261.72	1950.15	1153.94
90:1	4220.70	3738.75	2862.48	2468.16	1460.45
100:1	5210.75	4615.75	3533.93	3047.11	1803.03

Table 1 A.--Hectares - Size of Opening by D/H Ratio and Tree Height.

D/H Ratio	White Pine 85'	Maple 80'	Red Pine 70'	Aspen 65'	Spruce Fir 50' Jack Pine 50'
1:1	.21	.19	.14	.12	.07
2:1	.84	.75	.57	.49	.29
3:1	1.90	1.68	1.29	1.11	.66
4:1	3.38	2.99	2.29	1.97	1.17
5:1	5.27	4.67	3.57	3.08	1.83
6:1	7.59	6.73	5.15	4.48	2.63
7:1	10.33	9.15	7.01	6.04	3.57
8:1	13.50	11.95	9.15	7.89	4.67
9:1	17.09	15.13	11.58	9.99	5.91
10:1	21.09	18.68	14.30	12.33	7.30
20:1	84.35	74.72	57.21	49.32	29.19
30:1	189.79	168.12	128.71	110.98	65.67
40:1	337.40	298.87	228.82	197.30	116.75
50:1	527.19	466.99	357.54	308.29	182.42
60:1	759.15	672.47	514.86	443.93	262.68
70:1	1033.29	915.31	700.78	604.25	357.54
80:1	1349.61	1195.50	915.31	789.21	446.99
90:1	1708.09	1513.05	1158.43	998.85	591.04
100:1	2108.76	1867.97	1430.16	1233.15	729.68

Table 2.--Birds of Upland Openings

	Large Opening	Small Opening	Edge	Forest
Turkey Vulture(*Cathartes Aura*)	—	—	—	—
Sharp Shinned Hawk(*Accipter striatus velox*)		—	—	—
Red Tailed Hawk(*Buteo jamaicensis*)	—	—	—	
Broad-winged Hawk(*Buteo platypterus*)			—	—
Rough-Legged Hawk(*Buteo lagopus*)	—			
Marsh Hawk(*Circus cyancus*)	—	—		
Kestrel(Sparrow Hawk)(*Falco sparverius*)	—	—	—	
Sandhill Crane(*Grus canadensis*)	—	—	—	—
Killdeer(*Charadrius vociferus*)	—			
Upland Sandpiper(*Bartramia longicauda*)	—			
Herring Gull(*Larus argentatus*)	—			
Ring Billed Gull(*Larus delawarensis*)	—			
Mourning Dove(*Zenaidra macroura*)	—	—	—	
Snowy Owl(*Nyctea scandiaca*)	—	—		
Hawk Owl(*Surnia ulula*)		—	—	
Short-eared Owl(*Asio flammeus*)	—	—		
Whip-poor-Will(*Caprimulgus vociferus*)		—	—	—
Night Hawk(*Chordeilis minor*)	—	—	—	—
Chimney Swift(*Choetura pelagica*)	—	—	—	—
Ruby throated Hummingbird(*Archilochus colubris*)		—	—	
Flicker(*Colaptes auratus*)	—	—	—	—
Downy Woodpecker(*Dendrocopus pubescens*)		—	—	—
Eastern Kingbird(*Tyrannus tyrannus*)	—	—	—	
Phoebe(*Sayornis phoebe*)	—	—	—	
Least Flycatcher(*Empidonax minimus*)		—	—	—
Horned Lark(*Eremuphilia alpestris*)	—			
Tree Swallow(*Iridoprocne bicolor*)	—	—		
Bank Swallow(*Riparia riparia*)	—	—	—	—
Rough-winged Swallow(*Stelgidopteryx ruficollis*)	—	—	—	—
Barn Swallow(*Hirundo rustica*)	—	—	—	
Cliff Swallow(*Petrocheliden pyrrhonota*)	—	—	—	
Purple Martin(*Progne subis*)	—	—	—	
Bluejay(*Cyanocitta cristata*)	—	—	—	—
Raven(*Corvus corax*)	—	—	—	—
Crow(*Corvus brachyrhynchos*)	—	—	—	—
Black Capped Chickadee(*Parus atricapillus*)		—	—	—
House Wren(*Troglodytes aedon*)		—	—	
Catbird(*Dumatella carotinensis*)		—	—	
Brown Thrasher(*Toxostoma rufum*)		—	—	
Robin(*Turdus migratorius*)	—	—	—	—
Eastern Bluebird(*Sialis sialis*)	—	—	—	
American Pipit(*Anthus spinoletta*)	—			
Cedar Waxwing(*Bombycilla cedrorum*)	—	—	—	
Northern Shrike(*Lanius excubitor*)	—	—	—	
Loggerhead Shrike(*Lanius ludovicians*)	—	—	—	
Starling(*Sturnus vulgaris*)	—	—	—	—
Black & White Warbler(*Mniotilta varia*)		—	—	—
Nashville Warbler(*Vermivora ruficapilla*)		—	—	
Yellow Warbler(*Dendroica petechia*)		—	—	
Yellow-rumped Warbler(*Dendroica coronata*)		—	—	—
Chestnut-sided Warbler(*Dendroica pensylvanica*)		—	—	
Mourning Warbler(*Oporornis philadelphia*)		—	—	
Northern Yellowthroat(*Geothlypis trichas*)		—	—	
Bobolink(*Dolichonyx oryzivorus*)	—			
Eastern Meadowlark(*Sturnella magna*)	—			
Western Meadowlark(*Sturnella neglecta*)	—			
Red-wing(*Aqelaius phoeniceus*)	—	—	—	
Rusty Blacbird(*Euphagus carolinus*)	—	—		
Brewer's Blackbird(*Euphagus cyanocephalus*)	—			

Table.--continued

	Large Opening	Small Opening	Edge	Forest
Common Grackle(*Quiscalus quiscula*)	—	—	—	
Cowbird(*Molothrus ater*)	—	—	—	—
Indigo Bunting(*Passerina cyanea*)		—	—	
Purple Finch(*Cardo purpureus*)		—	—	—
Pine Grosbeak(*Pinicola enucleator*)		—	—	—
Redpoll(*Acanthus flammea*)	—	—	—	
Pine Siskin(*Spinus pinus*)	—	—	—	
American Goldfinch(*Spinus tristis*)	—	—	—	
Rufous-sided Towhee(*Pipilo erythropthalmus*)		—	—	
Savannah Sparrow(*Passerculus sandwichensis*)	—			
Grasshopper Sparrow(*Ammodramus savannarum*)	—			
Vesper Sparrow(*Pooecetes gramineus*)	—			
Dark Eyed Junco(*Junco hyemalis*)		—	—	—
Tree Sparrow(*Spizella arborea*)		—	—	
Chipping Sparrow(*Spizella passerina*)		—	—	
Clay Colored Sparrow(*Spizella pollida*)		—	—	
Field Sparrow(*Spizella pusilla*)	—	—	—	
White-throated Sparrows(*Zonotrichia albicollis*)		—	—	—
Song Sparrow(*Melospiza melodia*)	—	—	—	
Lapland Lonspur(*Calcarius lapponicus*)	—			
Snow Bunting(*Plectrophenax nivalis*)	—			

groups corresponding to any plant associa- , but that "groups' readily overlap one her. F. James (1971), H. Shugart, and ames (1973), using modern statistical meth- have been able to locate birds along a con- um of vegetational structure from open try to forest association in Arkansas. stedt and Niemi (1974) have undertaken a ilar study in a burned over forest area in esota.

Unfortunately there are no known similar ies of upland openings in the northern States. The list of birds of upland ings (Table 2) is based on the observa- s of many persons (Taylor)[4/] in addition to lished accounts.

The distinction between birds of small ings and edge is poorly documented.

UPLAND OPENING MANAGEMENT

Nature provides upland openings, grassy shrubby, through such agents as fire, d, flooding (including beaver flooding), ects, disease, and the death of old trees.

Modern forest management discriminates inst these openings in several ways. For- fires are prevented or controlled. Mod- silviculture works to minimize loss of d through old age, insects and disease. ber harvest methods are scheduled to achieve ediate reestablishment of forest stands. e plantings are used where delay in re- ablishment is experienced or expected, and fill in nonstocked or partially stocked nds.

If openings are to remain a part of the est, the need for them must be recognized, their development, maintenance, and pro- tion planned.

In the Lake States, upland opening man- ement has been, and largely is, based on e recognized needs of game species. Large land openings - 200 acres (80 hectares) larger - are a special management situa- on to benefit sharptail grouse or geese.

Small forest openings are managed as a rt of the forest. The objective usually to maintain a percent of forest lands in e upland openings. The percent, from 1- , is based on a compromise with other manage- nt activities - often to favor a target species such as ruffed grouse, deer, kirtland's warbler, or sandhill crane.

The size of the openings vary from 1/2 (0.2 hectares) to 10 (4 hectares) acres; most are about 1 acre (0.4 hectares). Size may be based on a requirement for a particular species (as noted above), on tradition, opinion, or simply to complement other forest management activities.

Distribution of upland openings is usually planned to take advantage of an existing opening or situation which will require the least development costs, and to attain uniform distribution.

Management procedure is to maintain existing suitable openings and develop additional openings as needed. Methods used include timber harvest, hand cutting trees and shrubs, prescribed burning, use of herbicides and mechanical methods such as bulldozer and roller chopper. In the future livestock grazing may become important as a maintenance and development tool in the special management of large opening. With all treatment the objectives are to kill all woody vegetation and establish or reinforce the sod ground cover. Use of herbicide provides the best and most certain result.

UPLAND OPENING MANAGEMENT RECOMMENDATION AND RESEARCH NEEDS

In the absence of biological information about optimum size - forest type relationships, it is prudent to vary opening size (D;H ratio). Size variation (D/H ratio of 1:1 to about a D/H ratio of 20:1) will compensate for our lack of knowledge of the habitat requirement of the majority of animals of opening and edge, and minimize any trend to create monotype openings.

The variety of types of openings is as important as the size or number. Different arrangements of the vegetative life forms prove attractive to different species. The difference between an opening with bluebirds, flickers, or kestrels may be only the absence or presence of a snag or two.

Kingbirds may use stumps, firecharred (Pinkowski, 1977) or not (personal observation) for nesting. A clump of shrubbery may harbor nesting and feeding birds that would not otherwise be there. In their discussion of parklike areas, Hooper et al (1973) found that some plots had greater bird diversity than they expected, and they believed that clumped vegetation provided nesting and escape cover for more birds than could have been supported if this small amount of vegetation had been dispersed.

[4/] Taylor, Charlotte M., 1966-1978, eeding Bird Surveys on Two Routes in Michi- n's Upper Peninsula, (Unpublished).

In various bird studies emphasis generally has been on breeding birds; use by birds for other than breeding may well be overlooked - as examples, all the broad-winged hawk nests that Carlson (1976) found in his study areas were within 425' (130 meters) of a forest opening and most of them were much closer. Sandhill cranes nest in bogs, but do their feeding and bring their young to feed in the forest openings. Aerial feeding birds, such as nighthawks, are frequently seen over openings. The scavengers, crows, ravens, and vultures patrol the openings. Robins come for blueberries and short-eared owls for their food. Migrating finches feed on the forbs and shrubs. In considering the numbers and kinds of openings, all these uses should be recognized.

Openings should be planned to furnish particular life forms. To this end our present concern for seeding openings, or favoring various grass, grass-forb, or shrub associations needs to be expanded to provide other life form aspects, such as stumps, snags, hollow logs, fallen trees or standing trees.

Life forms of the forest not available elsewhere in the forest, such as sparse stands or park-like stands, should be provided as a part of upland opening management.

The description, or interpretation of life form is more basic to the understanding and management of nongame birds (and game birds), than are timber types or currently used forest vegetation designations. Development of procedures to interpret life form from type designation is desirable. The availability to interpret a vast amount of timber management data in terms of biomass of the various parts of a forest stand would be a giant step toward description of life form, with a minimum of additional effort. James (1971), Anderson and Shugart (1974), and Shugart and Patten (1972) have developed methods that could be utilized.

Livestock grazing has been mentioned as a tool. It may also become a reason for openings - this is still new so the effects it may have are speculative.

The partial list of the birds using these openings should be completed before grazing starts so that the effect of grazing on the birdlife can be assessed.

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EFFECT OF FOREST FRAGMENTATION ON BIRD POPULATIONS

Chandler S. Robbins 1/

Abstract.--Many of the insectivorous songbird species that winter in the tropics are dependent on large unbroken tracts of forest during the breeding season. These species are disappearing from localities where forests are becoming fragmented. By long-range planning, managers can prevent local extinctions of these area-sensitive birds through use of such techniques as management in large units, retention of connecting corridors, and prevention of excessive isolation of forest fragments. Edge conditions can be provided, where appropriate to meet the needs of upland game species.

INTRODUCTION

Birds are sensitive indicators of habitat conditions, because each bird species has its own distinctive breeding range and habitat requirements. Habitats can be managed to increase or decrease abundance of bird species, with information derived from correlating bird populations with quantitative descriptions of the habitats in which they nest. Likewise, the presence or even abundance of certain species can be predicted on the basis of geographical location and habitat descriptions (Robbins 1978).

The purpose of this presentation is to discuss a relatively new concept in forest management: the dependence of many of the neotropical migrants on extensive tracts of forest. Just as many species of birds are restricted to certain types of habitats (woodland, prairie, desert, tundra), some species are adapted to living in the interior of an extensive forest while others utilize habitat boundaries such as wood margins and hedgerows. Each species has evolved over thousands of years and its populations have reached a state of equilibrium within its particular preferred environment. When habitat conditions change as a result of plant succession, climatic changes, or various influences brought about directly or indirectly by man, the survival potential of the species changes. When these changes favor a species, the population may spread into the favorable habitats and increase in size. When altered habitat conditions result in increased mortality or lowered reproductive rate, the population will decline unless it can be supported by immigration from nearby areas where a high reproductive rate produces a surplus of individuals. If a supply of invading individuals is not available or is insufficient to make up for the deficit, the population may decrease to a new lower equilibrium or even disappear entirely from the region of altered habitat.

I first present the results of some recent studies relating changes in breeding bird populations to changes taking place in the environment. Following that I suggest some guidelines for management of forests to benefit those nongame bird species that are disappearing as a result of failure to take their needs into consideration.

AREA SENSITIVITY

In the eastern and north central forest regions of the United States, there are many species of birds that are dependent on extensive forest systems. In recent decades these species have been retreating in the face of fragmentation of forest by such impacts as suburban sprawl, super highways, transmission lines, reservoirs, and surface mining. These sensitive birds have all but disappeared from suburban and highly agricultural areas.

Bird students have been aware of the sharp decline in breeding populations of flycatchers , vireos, warblers, and other long-distance migrants in woodland in and near the

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District of Columbia (Criswell et al. 1978). These decreases have been attributed by various investigators to a variety of causes, including sewer and highway construction, predation, greater human use, storm damage, pesticides, and loss of habitat in the vicinity of the study plots and on the wintering grounds.

Ornithologists in both Europe and America have shown that more bird species can be found nesting in large study plots than in small ones (Oelke 1966, Moore and Hooper 1975). This conclusion seems obvious, because birds are patchily distributed in most habitats, which in itself is because most habitats are structurally heterogeneous. A major reason for increased avian diversity in larger tracts, however, was overlooked by these authors.

Bond (1957), who studied bird populations in woodlots in southern Wisconsin, was the first to report that many species of small songbirds are dependent on relatively large forest tracts during the breeding season. MacArthur and Wilson (1963, 1967) demonstrated the relation between oceanic island avifaunas and the size and degree of isolation of the islands. They also suggested that the same equilibrium between colonizations and extinctions might exist on fragmented woodlots. In oceanic or mainland models, the number of breeding species increases with "island" size and decreases with distance from sources of repopulation. Whitcomb (1977) has summarized MacArthur and Wilson's widely accepted equilibrium theory of island biogeography, and discussed its implications for biotic diversity. He pointed out that: (1) as many as 92 percent of the breeding birds in some forests are migratory, (2) most of these are area-sensitive species that cannot persist in the face of forest fragmentation, and (3) they are not replaced by other species.

New Jersey Studies

In 1972 Galli et al. (1976) and Forman et al. (1976) studied bird populations on 30 forest fragments in central New Jersey. They used analysis of variance to detect those species dependent on the size of the forest fragment. Their forests varied in size from 0.01 to 24 ha. Unfortunately they did not present comparable data from a large area of continuous forest for comparison with their forest fragments. Furthermore, only one of their fragments was greater than 10 ha in size. Although they concluded that half of the forest species using their study plots were dependent on forest area, those species that are most critically dependent on area were lacking from all of their plots and consequently were not recognized as being area dependent.

Sources of Maryland Data

During the breeding seasons of 1974-76, R. F. Whitcomb and colleagues undertook a more extensive study of area sensitivity of eastern deciduous forest birds (Whitcomb et al., 1979). Realizing the urgency of obtaining a broad base of bird population data from forested plots of many sizes and degrees of isolation, they used four techniques. Breeding Bird Census (Williams 1936) and Point Survey data (Whitcomb et al., 1979) from 30 forest fragments ranging in size from 1 to 121 hectares were supplemented with data obtained from the results of Breeding Bird Survey Miniroutes (Bystrak 1978) and a Breeding Bird Atlas project (Klimkiewicz and Solem 1978). They used bird counts from 185 Miniroute stops scattered throughout Howard County, Maryland, and 700 stops throughout Prince Georges County; each of these Miniroute points was covered twice. The Atlas data, gathered by members of the Maryland Ornithological Society, showed which species were detected in each of the 25 square kilometer blocks throughout Montgomery County and 6.25 square kilometer blocks throughout Howard County.

Characteristics of Area-sensitive Species

Whitcomb et al. (1979) computed an index of area sensitivity for each forest bird species by dividing the average number of territories detected at sampling points within small (6-14 ha) forest islands by the number detected in large (80+ ha) forest tracts. They noted strong correlations between the area sensitivity of many bird species and their regional distribution and abundance in forest habitats. When they compared area sensitivity of each forest bird species with characteristics of its breeding biology, they found that most of the species sharply reduced by forest fragmentation have the following characteristics: (1) they are long-distance migrants that winter primarily in the New World tropics; (2) they are obligate inhabitants of forest interior; (3) they tend to nest on or near the ground; (4) they build nests in the open rather than in the protection of cavities; (5) they raise only a single brood of young per year; and (6) they have a comparatively small clutch size.

In contrast, many bird species that reproduce successfully under forest edge conditions are permanent residents or short-distance migrants that arrive early in the season and attempt two or more broods per season. The average nest height of these species is greater, more of them nest in cavities, and they raise many more young per year. Because of a higher reproductive potential, edge-inhabiting bird species have a much greater chance of reproductive success in areas where predation from mammals, jays, and grackles is higher, nest parasitism from cowbirds is more frequent, and disturbance from humans is higher. On the other hand, some neotropical migrants that specialize in edge or scrub habitat (e.g., Prairie Warbler, Orchard Oriole, Blue Grosbeak) show some of the same tendencies for lower reproductive effort and higher sensitivity.

Area Sensitive Species

The area-sensitive forest interior species recognized by Whitcomb et al. (1979) include not only the Yellow-billed Cuckoo, Wood Thrush, Red-eyed Vireo, Black-and-white Warbler and Scarlet Tanager recognized by Galli et al. (1976), but also the Whip-poor-will, Pileated Woodpecker, Acadian Flycatcher, Veery, Yellow-throated Vireo, Worm-eating Warbler, Northern Parula Warbler, Ovenbird, Louisiana Waterthrush, Kentucky Warbler, Hooded Warbler, and American Redstart, as well as such wide-ranging species as hawks and owls.

Effects of Forest Fragmentation

A few specific examples will emphasize the dependence of area-sensitive species on large tracts of undisturbed forest interior, tracts greatly in excess of the 1-5 ha territory size actually defended by most small migratory nongame birds during the breeding season. The following examples are based on 3 long-term studies in which I have involved, and 3 long-term Breeding Bird Censuses published in American Birds.

Laurel

In 1952, I moved into my present home beside the Patuxent River gorge on the outskirts of Laurel in central Maryland. At that time the forest along the river was interrupted 3/4 km below me by the City of Laurel, but continued essentially unbroken for 14 km upstream (fig. 1a). The contiguous forest totaled about 5260 ha at that time, but it became progressively more fragmented during the ensuing 25 years. First, Rocky Gorge Reservoir was created 3/4 km upstream from my home; next, Interstate 95 was constructed between my home and the reservoir; and then the hillside directly across the river was cleared of trees (fig. 1b).

Although my woods and the remaining contiguous area of forest totaling about 40 ha have not changed appreciably in character, half of the long-distance migrants that nested here 25 years ago have disappeared: Broad-winged Hawk, Whip-poor-will, Yellow-throated Vireo, Black-and-white Warbler, Worm-eating Warbler, Ovenbird, Louisiana Waterthrush, Kentucky Warbler, and Hooded Warbler (table 1). The Acadian Flycatcher, Eastern Wood Pewee, Wood Thrush, Red-eyed Vireo, Northern Parula Warbler, and Scarlet Tanager still nest here nearly every year, but in reduced numbers; and one pair of Red-shouldered Hawks still remains--perhaps

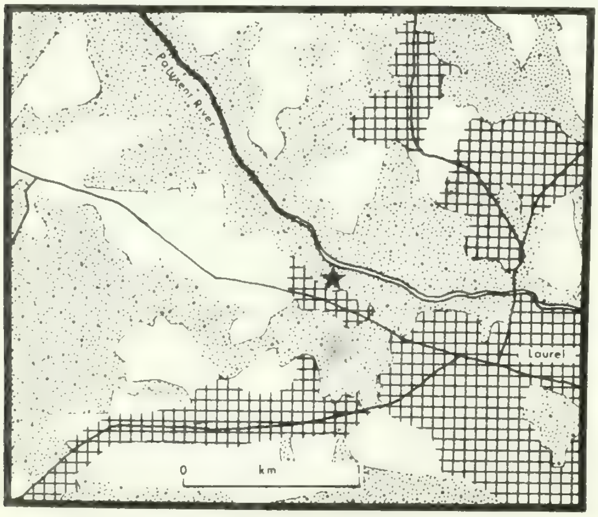


Figure 1a.--Vicinity of Laurel, Maryland, showing forest cover (dots), fields (white), urban areas (small squares), and main highways (black lines) as indicated in 1951. Woods referred to in the text are marked with a star. (USGS 7.5-min. Laurel, Md., quadrangle, 1951)

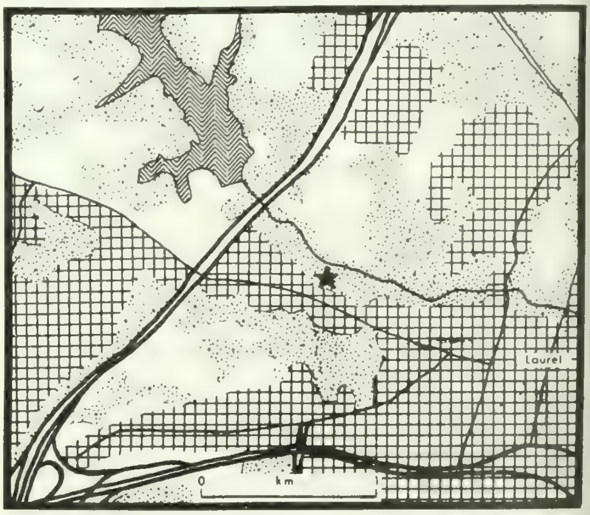


Figure 1b.--Same area in 1971, showing Rocky Gorge Reservoir, Interstate Route 95, Maryland Route 198 (bottom), and severe fragmentation of woodland. (USGS 7.5-min. topographic map, 1965, photorevised 1971)

Table 1. Population changes of long-distance migrants

Site	Laurel		Cabin John		Rock Creek		Glover-Archbold		Seton Belt		Patuxent WRC	
Plot size (acres)	--		18.75		80	65	35		36		90	135
Forest area (acres)	13,000	100	200	75	850		185		39		7400	
Years	1953 -54	1977 -78	1947 -48	1976 -77	1948 -49	1974 -77	1959 -60	1976 -77	1947	1975 -76	1959	1972
Broad-winged Hawk	X[1]	0										
Yellow-billed Cuckoo	X	X	5.0	0	1.0	0			3.0	1.5	0	3.0
Whip-poor-will	X	0										
Ruby-throated Hummingbird	X	X	5.0	0	3.0	0			4.0	+[2]	2.0	1.5
Great Crested Flycatcher	X	X	14.5	5.0	4.5	+	14.0	0	8.0	0	0	0.5
Acadian Flycatcher	X	X	34.5	34.5	27.0	1.0	25.5	3.0	33.0	18.1	25.0	14.5
Eastern Wood Pewee	X	X	26.5	8.0	7.0	2.0	8.5	1.0	19.0	20.1	4.0	0.5
Wood Thrush	X	X	21.5	0	20.0	8.5	32.0	4.5	40.0	81.9	20.5	14.0
Veery					0	5.5	40.0	57.5			0	+
Yellow-throated Vireo	X	0	9.5	0	8.0	0	3.5	0	19.0	2.1	2.0	3.5
Red-eyed Vireo	X	X	74.5	40.0	52.0	18.5	31.5	12.5	100.0	92.4	50.0	50.5
Black-and-white Warbler	X	0	V[3]	0	3.5	0			11.0	0	3.5	0
Worm-eating Warbler	X	0	V	0					3.0	0		
Northern Parula Warbler	X	X	70.5	8.0	0.5	0	11.5	0	4.0	+	3.5	2.0
Ovenbird	X	0			49.0	12.0	8.5	2.0	53.0	22.9	14.5	8.5
Louisiana Waterthrush	X	0	5.0	0	0	0.5	+	0			4.5	2.0
Kentucky Warbler	X	0	28.0	0	1.0	0	8.5	0	17.0	9.7	11.0	5.0
Hooded Warbler	X	0	11.0	0	5.0	0	15.0	0	8.0	1.4	19.0	0.5
American Redstart			68.0	13.5			34.0	+			9.0	7.0
Scarlet Tanager	X	X	13.5	0	9.0	6.5	8.5	0	26.0	12.5	15.5	7.5
Mean species per year	-	-	31.0	21.5	26.5	21.5	42.0	26.5	28.0	25.5	32.0	47.0
Percent change in species	-50%		-31%		-19%		-37%		- 9%		+47%	
Mean pairs/100 acres	-	-	658.5	364.0	223.1	126.9	718.6	453.6	437.0	390.3	289.4	260.5
Change in total population	-		-45%		-43%		-37%		-11%		-10%	
Pairs of long-distance migrants/100 acres	-	-	387.0	109.0	190.5	54.5	232.5	80.5	348.0	262.6	184.0	120.5
Change in long-distance migrants	-		-72%		-71%		-65%		-25%		-35%	

[1] X = Present, but density not determined
[2] + = Present in very small numbers, less than one-half territory
[3] V = Visitor, not nesting in study plot

receiving recruitment from the thriving population on the Patuxent Wildlife Research Center 8 km downstream.

Cabin John Island

A second example of a drastic change in bird population is evident on Cabin John Island in the Potomac River 4 km northwest of Washington, D. C., where breeding bird populations have been studied almost annually since 1947. This island is more than 500 m long and has an average width of 150 m (fig. 2a). Although vegetation of the island itself has not changed appreciably during the study period, there has been significant road construction, particularly the George Washington Memorial Parkway on both sides of the river, that has fragmented the formerly continuous forest that flanked both shores (fig. 2b). Many of the other nearby forests have yielded to housing developments.

During the 30-year study, five species that had originally been represented by two or more breeding pairs disappeared completely. These were the Wood Thrush, Yellow-throated Vireo, Kentucky Warbler, Hooded Warbler, and Scarlet Tanager. Three other less common species, the Yellow-billed Cuckoo, Ruby-throated Hummingbird, and Louisiana Waterthrush, also disappeared (table 1). Several other species declined 46% or more: Great Crested Flycatcher, Eastern Wood Pewee, White-breasted Nuthatch, Red-eyed Vireo, Northern Parula Warbler, and American Redstart (Thatcher 1948, Criswell and Gauthey 1977, and Criswell et al. 1948). The only neotropical

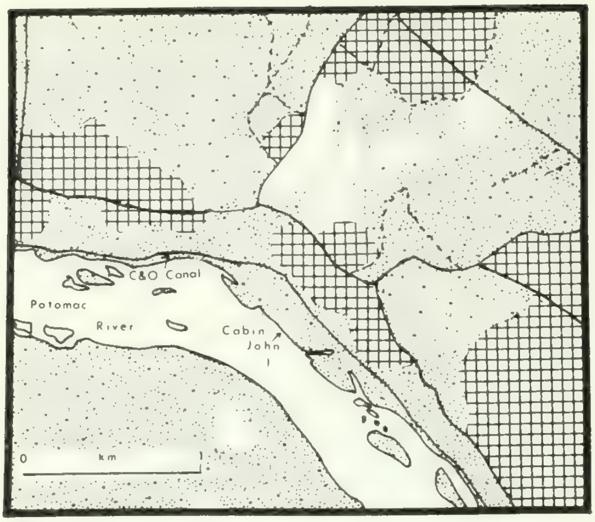


Figure 2a.--Vicinity of Cabin John Island as shown in 1951. (USGS 7.5-min. Falls Church, Va.-Md. quadrangle, 1951) Shading as in figure 1.

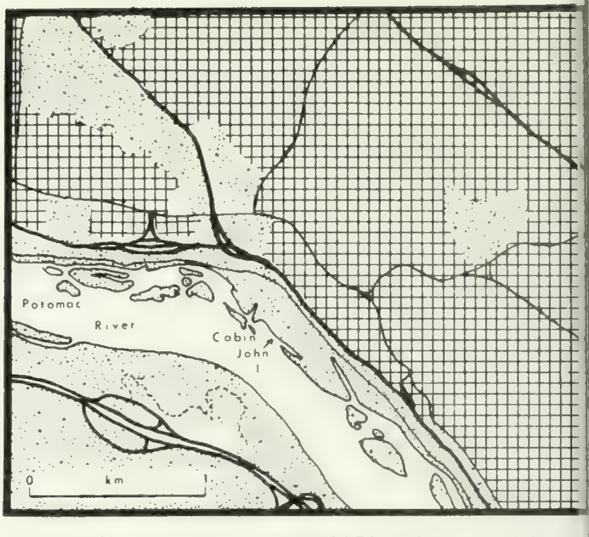


Figure 2b.--Same area in 1971, showing urban expansion and fragmentation of forest by major highways. (USGS 7.5-min. Falls Church, Va.-Md. quadrangle, 1965, photo-revised 1971)

migrant that did not decrease from 1947-48 to 1976-77 was the Acadian Flycatcher.

Rock Creek Park

Two similar long-term studies have been conducted in Rock Creek and Glover-Archbold parks, major wooded areas within the District of Columbia. Rock Creek Park is a long, narrow area of about 800 ha along Rock Creek. It is completely surrounded by city and for many years has not been connected to the narrow strip of forest along the Potomac River by even a wooded corridor. Near the center of Rock Creek Park is a 26 ha study plot in which breeding birds have been censused intermittently since 1947. The original study plot (32 ha) was part of a 345 ha tract bordered on the north by Military Road and on the south by Porter Street. Beach Drive, Glover Road, Tilden Street, and several minor roads traverse the 345 ha wooded tract, but the total amount of contiguous woodland present has changed very little during the 30-year period of the study. Automobile traffic and pedestrian use has increased in both the study plot and the Park in general. Comparing (table 1) the early studies of Thatcher (1949) with more recent studies by Craven et al. (1974) and Criswell et al. (1978) one notes that the Yellow-billed Cuckoo, Ruby-throated Hummingbird, Yellow-throated Vireo, Northern Parula Warbler, Kentucky Warbler, and Hooded Warbler no longer breed in the study plot. Other species that have decreased by more than 50% during this period are the Great Crested Flycatcher, Acadian Flycatcher, Eastern Wood Pewee, Wood Thrush, Red-eyed Vireo, and Ovenbird. Recent surveys indicate that changes in bird population recorded within th plot are characteristic of the entire Rock Creek Park forest system.

Glover-Archbold Park

Glover-Archbold Park and adjacent wooded areas make up about 75 ha of woodland that ar connected by a narrow corridor to the fringe of woods along the Potomac River. Breeding birds in the park have been censused annuall since 1959 (Briggs 1960, 1961, 1977, 1978). Except for the results of sewer construction in 1963, there has been no major change in th habitat of the study plot.

Neotropical migrants that were found nesting on the 14 ha study plot in 1959 or 1960 but were absent in 1976 and 1977 were Broad-winged Hawk, Great Crested Flycatcher, Yellow-throated Vireo, Northern Parula Warbler, Kentucky Warbler, Hooded Warbler, an Scarlet Tanager. The following additional species decreased more than 60% during the same period: Acadian Flycatcher, Eastern Woo Pewee, Wood Thrush, Red-eyed Vireo, Ovenbird, and American Redstart.

Seton Belt Mature Woodlot

In 1947, Stewart and Robbins (1947) censused the breeding bird population in a 15 ha plot within a fine stand of about 16 ha of mature tulip-tree--oak forest in southern Prince Georges County, Maryland. The results showed an exceptionally high density of breeding birds, 1,080 territorial males per square km. It is believed to be the largest remnant of nearly virgin forest on the coastal plain of Maryland.

Whitcomb et al. (1977) censused this woodlot again in 1975 and 1976 using the same boundaries and techniques as in 1947. Their report includes a map showing the location of this South Tract plot with relation to highways and nearby woods. The changes in density of neotropical migrants are much less than in the other plots studied (table 1).

Patuxent Wildlife Research Center

In 1959, I censused the breeding bird population in an undisturbed 36 ha portion of the mature deciduous forest along the Patuxent River in Prince Georges County, Maryland. The census plot was a mosaic of well drained and poorly drained floodplain with small islands of the neighboring river terrace, into which one-third of the plot projected. This plot, by virtue of its size, lack of disturbance, habitat diversity, and location within a 3000 ha forest on the Patuxent Wildlife Research Center and adjacent Fort George G. Meade, contained the entire avian species pool of the eastern deciduous forest of coastal plain Maryland. Breeding populations of the neotropical migrants are listed in table 1; for populations of the other species see Stamm et al. (1960). The bird population was subsequently sampled annually by 12 days of mist netting each summer through 1972, and breeding bird censuses were repeated every few years.

Timber was not cut in or near the study plot; however, all of the following disturbances probably contributed to the change in avian populations shown in table 1: (1) One corner of the plot was permanently flooded by construction of a duck pond in a nearby field; in addition to loss of forest from the study plot itself, the flooding brought an array of edge species (plant and animal) into the plot. (2) Construction of Rocky Gorge Reservoir upstream just before the beginning of the study altered the flooding regime of the tract; instead of being inundated periodically for short intervals several times each year, the water table is lower and the floods are fewer but more catastrophic. (3) Effluent from the Laurel sewage treatment plant now provides a substantial part of the total flow of the Patuxent River during the summer months. (4) In 1962, as part of a simulated pesticide study, 174 breeding birds including 169 individuals of neotropical species were netted and removed from the plot to study the rate of repopulation. The intent was to return the removed birds to the plot; however, the cooperating agency that was caring for the birds could not keep them alive and thus none of the warblers and flycatchers survived.

The density of neotropical migrants decreased during this study (table 1), but only one breeding species disappeared entirely: the Black-and-white Warbler.

The Pattern

The pattern is quite clear. It is essentially the same group of species that are declining in each study plot, and these birds are the long-distance migrants. The permanent resident species, on the other hand, tend to maintain their populations despite suburban sprawl and forest fragmentation; the short-distance migrants that have adapted to survival in edge habitats, such as jays, House Wrens, catbirds, robins, starlings, blackbirds, and towhees, also are maintaining their populations.

Summarizing table 1 (in which the data are presented in the original English measurements of the investigators): there was an overwhelming decrease in every long-distance (neotropical) migrant except the Veery; there was a decrease in density of breeding birds in every plot, even those with minimum disturbance; and the percentage decrease in long-distance migrants was consistently much greater than the decrease in the total population. If the densities of long-distance migrants are subtracted from the total densities, the sum of the densities of permanent residents and short-distance migrants in five plots (no densities are available from Laurel) dropped from 984.5 in the early studies to 968.2, a decrease of only 1.7%.

The only species that showed increases in any of the study plots in table 1 (out of 96 pairs of observations) were the following: Great Crested Flycatcher and Yellow-throated Vireo, both present in very small numbers, increased at Patuxent; the vireo was present every year, while the flycatcher nested erratically. There were very small increases in the Eastern Wood Pewee on the Seton Belt tract and the Red-eyed Vireo at Patuxent. The Wood Thrush increased substantially on the Seton Belt tract. The Veery, a recent invader from more northern breeding grounds, established itself or increased on three plots. The Louisiana Waterthrush increased by a fraction of a territory in Rock Creek Park.

A Sample Species, the Worm-eating Warbler

Let us consider briefly the breeding distribution in Maryland of one of the species that no longer nests in any of the study plots in figure 1, the Worm-eating Warbler. The map in Birds of Maryland and the District of Columbia (Stewart and Robbins 1958) showed this species as nesting throughout the Ridge and Valley, Piedmont, and Western Shore

Coastal Plain Sections except for the highly agricultural Hagerstown, Middletown, and Frederick valleys and the flat bayshore necks of Baltimore, Harford, and Cecil counties. It also nested in forested areas along the Pocomoke River and its main tributaries and at seven isolated spots elsewhere in the State. A portion of the present-day distribution, based on the Breeding Bird Atlas of the Piedmont counties of Montgomery and Howard (Klimkiewicz and Solem 1978), is shown in figure 3. This species is strictly limited to the few remaining areas of extensive woodland.

Supporting Evidence from Breeding Bird Survey

To further test the area sensitivity of forest species and to gather information on the minimum forest area required to maintain populations of various species, comparisons were made between bird counts and habitat factors at 500 Breeding Bird Survey (Robbins and Van Velzen 1969) stops scattered through central and eastern Maryland. Each 3-minute Breeding Bird Survey stop was visited annually in the early morning in June, and data for 1974-78 were used in the analysis. Thirty habitat characteristics were recorded at each stop. One of these was a measure of the acreage of contiguous forest in and adjacent to the quarter-mile radius counting circle. I should stress that the measurement of amount of woodland included not just the wooded area within the quarter-mile circle, but it also included all contiguous forest connected to woodland within the counting circle. For purposes of the analysis the forest was categorized into units expressed as powers of three. For example, forest plots of less than 3 acres (1.2 ha) were coded 0, those between 3 and 3^2 (3 to 9 acres, 1.2 to 3.6 ha) were coded 1, those between 3^2 and 3^3 (9 to 27 acres, 3.6 to 10.9 ha) were coded 2, etc. The highest category encountered was coded 8 (between 6,561 and 19,683 acres, 2,655 and 7,966 ha).

Correlation coefficients were computed for 72 bird species; the recorded abundance of each bird at each stop (5-year sum) was matched against each of the following habitat factors: percentage of coniferous, deciduous, and mixed woods within a circle of 400 m (one-quarter mile) radius, and height of the canopy; percentage of brush, plowed, cultivated, pasture, hay, lawn and fallow land, and of tidal estuaries, salt, brackish, and fresh marsh, and disturbed or industrial areas; number of houses and of visible snags; presence of hedges, electric wires, fences, streams and

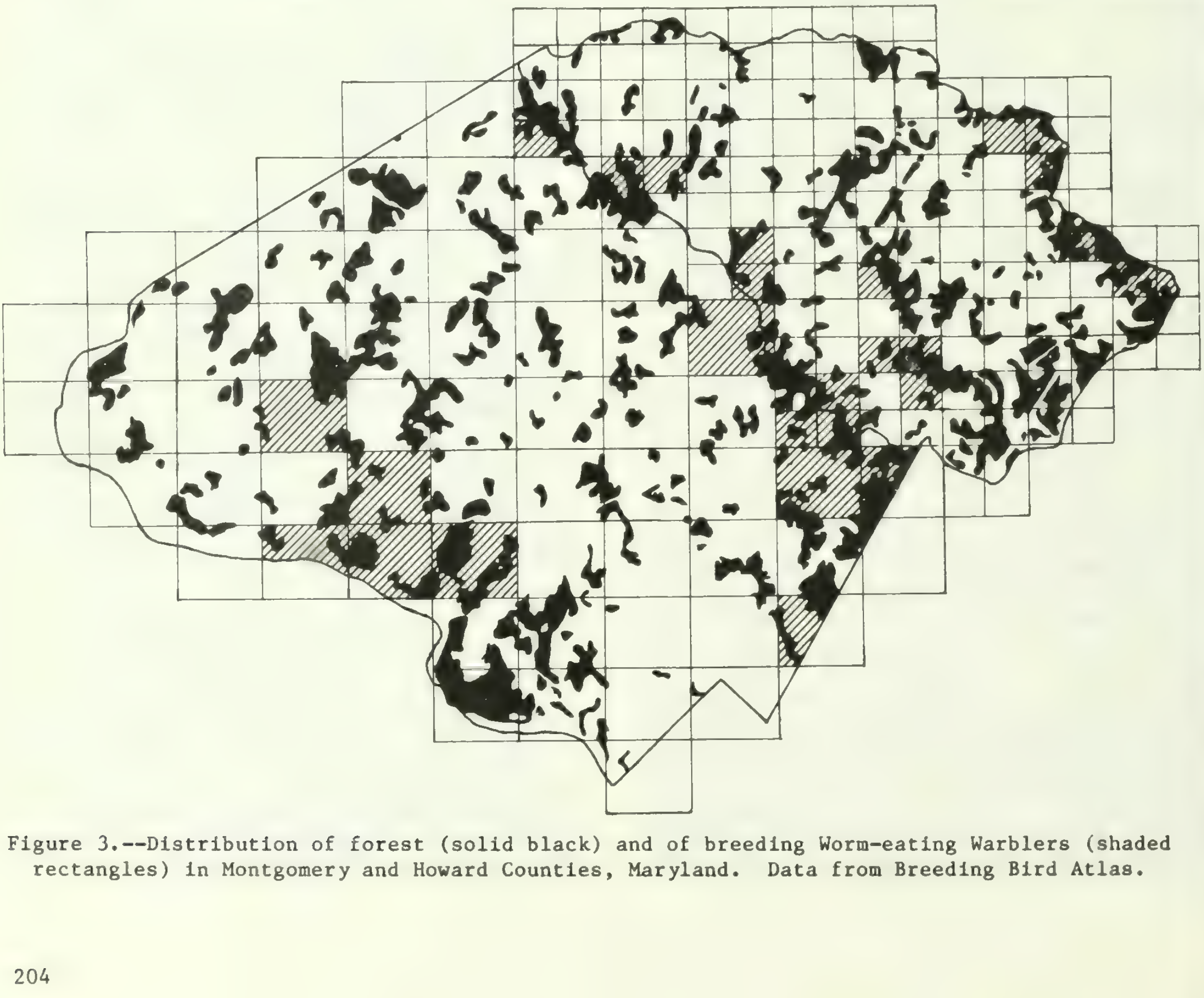


Figure 3.--Distribution of forest (solid black) and of breeding Worm-eating Warblers (shaded rectangles) in Montgomery and Howard Counties, Maryland. Data from Breeding Bird Atlas.

ponds; height of shrubs and width of roadside shoulder; also whether the road was paved, the time of morning when the bird counts were made, and the area of contiguous forest as described in the previous paragraph.

Considering only those correlations that were highly significant ($p < .01$) when each bird species was compared with each of 29 environmental factors, the only factor that was correlated with the abundance of more than half of the bird species was the area of contiguous forest (41 species). Other factors with a large number of highly significant correlations were: percentage of deciduous woods (36 species), percentage of coniferous woods, percentage of mixed woods and number of houses (24 species each), percentage of hayfield (23 species), and presence of fences (22 species).

Supporting Evidence from the Allegheny Mountains

In the Allegheny Mountains of Western Maryland and Western Pennsylvania, Deanna Dawson and colleagues from the Migratory Bird and Habitat Research Laboratory studied breeding bird populations with relation to numerical habitat descriptions in the summer of 1978. They included in their list of variables the same area measurement of contiguous forest that I had used in the above Breeding Bird Survey analyses. Their habitat variables were measurements of the tree size and density, shrub cover, canopy cover, ground cover, tree species, slope, and other criteria almost entirely different from those used in the Breeding Bird Survey analysis. It is important to note, however, that the one factor with the largest number of significant correlations with bird populations was the same one that was most significant in the Breeding Bird Survey analysis--the area of contiguous woodlands.

Determining Area Requirements for Sensitive Species

Problems in Making Estimates

Having established that a strong relationship exists between the extent of contiguous woodland and the populations of certain species of birds, the next question is one of defining the amount of contiguous forest needed for each of the area-sensitive species. Rough estimates can be obtained in several ways. One is to find the smallest forest fragment on which the species maintains at least one territory during the nesting season. The chief problem with this approach is that it does not take isolation into account. For example, MacClintock et al. (1977) found that a small fragment minimally isolated from a large continuous forest supported many of the neotropical migrant species characteristic of the larger woodland. Howe and Jones (1977) also pointed out that the least isolated of the small woodlots in southern Wisconsin supported the most species. Thus, any given small woodland is an integral part of a regional habitat mass that supports a regional population of the species in question. Subunits of this regional habitat mass are inadequate, by themselves, to support a population of sufficient size to retain genetic flexibility and to buffer against normal oscillations that characterize all populations. Also, it is difficult or impossible to know whether a given nesting attempt is successful, or even whether a singing male has a mate. Furthermore, it would be dangerous to draw conclusions from a single observation, which might be atypical. A pair of birds may succeed in rearing young in a year of super-abundant food. In years when food is in short supply, weather is abnormally wet, or predation is exceptionally high, nesting might be a complete failure. Thus, the critical area required for survival of an area-sensitive species is the area in which young can be produced in sufficient numbers to replace adult attrition under the poorest conditions of weather, food availability, competition from other wildlife, and other disturbances. All in all, the diversity of interacting factors presents a complex situation, and the investigator must exercize extreme caution in proposing "safe" definitions of forest area required.

Estimates from Breeding Bird Survey

To approach the problem in another way, I have computed for each area category the percentage of Breeding Bird Survey stops at which each area-sensitive species was recorded, using 5 years of data from 500 roadside stops in central and eastern Maryland. In this way I can determine not only the smallest forest fragment in which the species was recorded, but can determine at what point the frequency of occurrence begins to decrease as contiguous forest area decreases. Admittedly this method is biased to some degree by the proportion of the quarter-mile circle that is wooded, regardless of whether the woods are continuous or fragmented. In spite of this bias, there is for each of the area-sensitive species at least one point at which there is a noticeable decrease in frequency of occurrence. The percentage of stops at which Kentucky Warblers were found, for example, remained constant at about 13% at stops with 33 or more ha of contiguous forest, but dropped abruptly in smaller woodlots (fig. 4). The Ovenbird was found in the great majority of the very extensive forests, but was much less frequently recorded in the 885

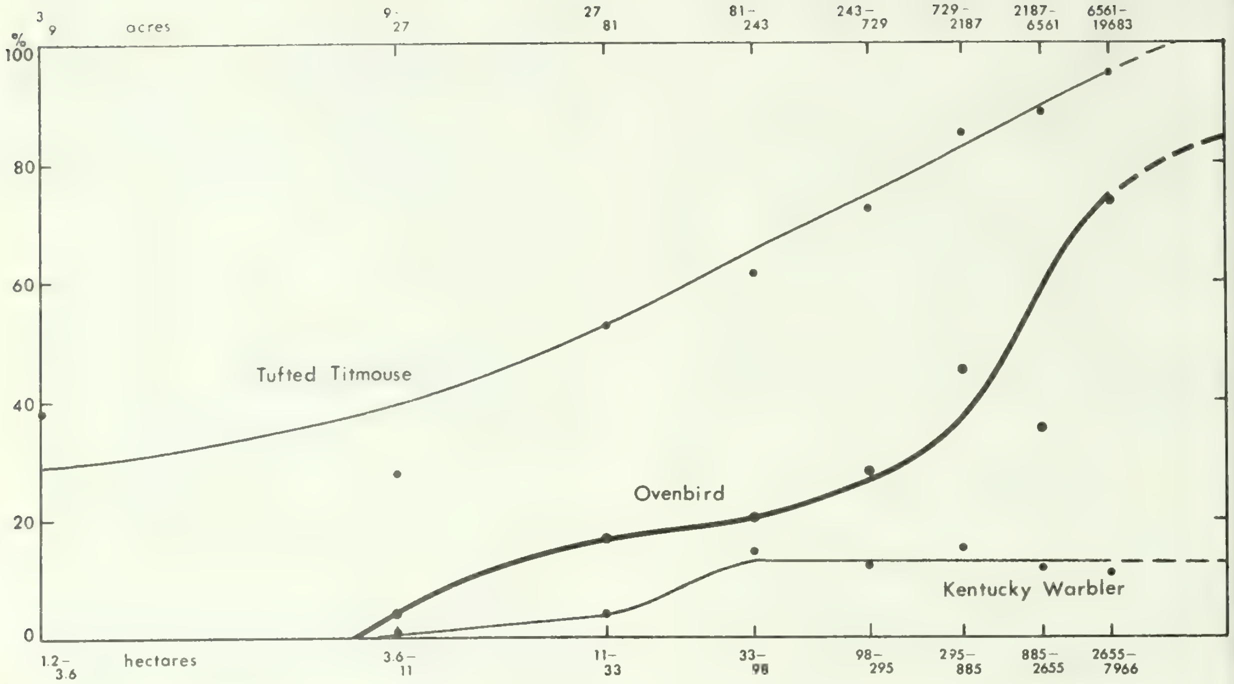


Figure 4.--Percentage of Breeding Bird Survey stops at which Tufted Titmouse, Ovenbird, and Kentucky Warbler were recorded. Stops are grouped according to the largest acreage of contiguous woodland present.

to 2,655 ha range; it was noted at nearly 20% of the stops with 11 to 98 ha of contiguous woodland, but at very few of the smaller woodlots (fig. 4). By comparison, the Tufted Titmouse, which is a permanent resident, did not show a sharp decline at any size class, and was present in woodlots of less than 3 ha. The size classes at which the frequency of occurrence of many of the area-sensitive species shows a sharp decline are presented in table 2, to give a preliminary estimate of the area sensitivity of each species.

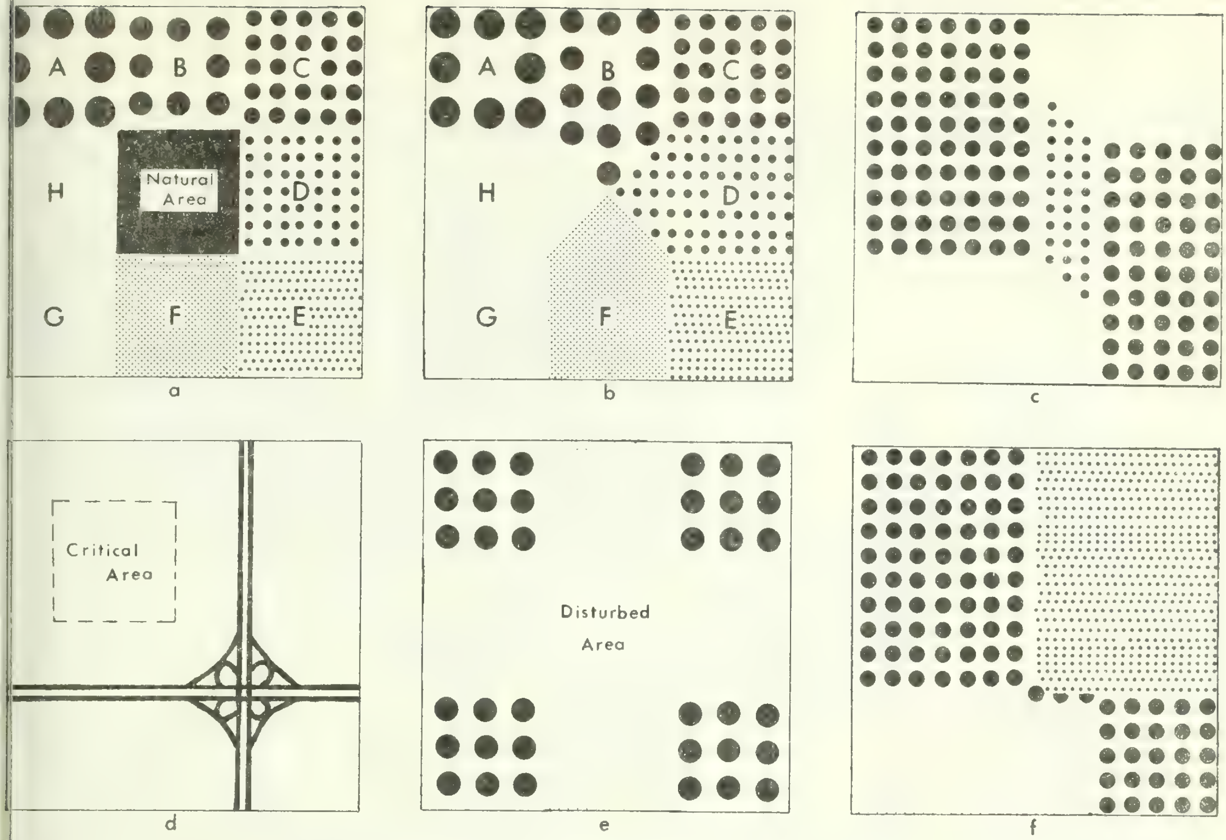
From other breeding population data we know that figures in table 2 for the Worm-eating and Hooded Warblers are lower than the size these species require. This discrepancy results from an inadequate sample size for these species. Several of the other species registered an additional sharp decline at a lower size level: Ovenbird at 10 ha (fig. 4), and Wood Thrush and Red-eyed Vireo at 4 ha. The management concept shown by these studies is that large blocks of forest are necessary for the survival of entire nongame bird communities.

MANAGEMENT IMPLICATIONS

General Management Principles

From these early studies on forest fragmentation we can make some recommendation for management of forests to maintain or possibly increase the regional bird species pool. Some of these recommendations are counter to traditional game management approaches of opening up the forest to provid more shrub growth for deer or Ruffed Grouse. Openings do provide more food for certain species, most especially for support of seed-eating birds through the winter, but suc openings as are desired for management of special interest species can be put in areas where they will not jeopardize a forest interior ecosystem.

First, a large undisturbed forest area needs to be maintained at all times. Where managed forests are contiguous with large natural areas (fig. 5a), such natural areas could serve as a nucleus for population maintenance. When the entire forest is subject to management, it is probably preferable to use a timber harvest rotation program under which a large contiguous tract remains undisturbed at any one time. Ideally,



igure 5.--Management implications for forests surrounded by other land use. Shading simulates age of forest.

- a) Ideal management, with best opportunity to preserve all bird species present.
- b) Good management, providing maximum adjacent habitat of each seral stage.
- c) Avifauna can be preserved by planting to connect isolated woods with other forest.
- d) Presence of highways or other disturbance requires change in management strategy.
- e) Severe fragmentation leads to extinction of area-sensitive species.
- f) Effects of fragmentation can be reduced by leaving connected wooded corridors.

arvest would occur in an orderly manner, such s a circular path (A, B, C, etc., in fig. 5b) ith several hundred hectares cut in 1 or 2 ears. The adjoining area would be cut everal years later, and so on, in such a ashion that the bird population would move rom one managed area to an adjacent one as he various seral stages moved across the andscape and as the area of mature forest radually moved from one spot to another.

Robert Whitcomb (pers. comm.) has pointed ut that when running Breeding Bird Survey outes in the West Virginia mountains he has een impressed with the great variety and bundance of warblers in areas heavily umbered and disturbed by strip mining. lthough most of the woods are in early and iddle stages of growth, management has been n large units and the avian species pool has een preserved. Another advantage of managing orests in units of several hundred hectares s that disturbance in any given season is estricted to a small part of the entire anagement area. Conversely, if timber is harvested in many small isolated plots in the same season, the operations will impact not only the birds in the several plots, but also those along many access trails in other portions of the management area. Aesthetically, management of much smaller units might be more pleasing; but if we wish to maintain the integrity of the entire ecosystem, fragmentation into small blocks (fig. 5e) should be avoided where possible.

In states where forests are already greatly fragmented, one should view a forest management plan in the context of the adjoining forest areas and strive to coordinate management practices with nearby land owners to prevent inadvertent loss of area-sensitive species through simultaneous destruction of sources of avian repopulation.

These recommendations are derived from research on bird populations; however, they might apply to other forms of life as well. Special management techniques should be considered for locally sensitive species.

Table 2. Preliminary estimates of minimum forest areas required to sustain viable breeding populations of area-sensitive forest birds, based on 500 Breeding Bird Survey stops in central and eastern Maryland.

Species	Frequency[1]	Critical size[2]	
		Acres	Hectares
Red-shouldered Hawk	14	250	100
Red-bellied Woodpecker	225	10	4
Hairy Woodpecker	22	10	4
Great Crested Flycatcher	146	25	10
Acadian Flycatcher	53	80	30
Eastern Wood Pewee	127	10	4
Blue Jay	262	10	4
Tufted Titmouse	294	10	4
Carolina Wren	300	25	10
Wood Thrush[3]	304	250	100
Yellow-throated Vireo	27	250	100
Red-eyed Vireo[3]	276	250	100
Black-and-white Warbler	24	750	300
Prothonotary Warbler	9	250	100
Worm-eating Warbler[3]	9	750	300
Northern Parula Warbler	19	250	100
Pine Warbler	71	80	30
Ovenbird[3]	84	6550	2650
Louisiana Waterthrush	6	250	100
Kentucky Warbler[3]	32	80	30
Hooded Warbler[3]	17	80	30
Scarlet Tanager	133	250	100
Summer Tanager	45	250	100

[1] Number of stops at which the species was found.
[2] Area at which the sharpest decrease occurred.
[3] See text for comment.

Snags

During the past 6 years several investigators have emphasized the value of snags to wildlife (e.g., see Conner 1978). There is no question that presence of snags will increase populations of hole-nesting species, especially in the early successional habitats containing few natural cavities. Snags also are used as perches for many species other than cavity nesters. Although snags increase the populations of some species, they may cause a decrease in others by introducing edge conditions into a forest interior. I doubt that anyone will challenge the benefits of leaving snags at or near the edge of a managed forest, but one must consider the consequences of permitting snags to be retained intentionally in forest interior situations. The principal problem is that snags are used by cowbirds for watching the activities of other species in whose nests they will lay their own eggs. Brown-headed Cowbirds have been increasing steadily since at least the mid-1960's (Bystrak and Robbins 1977), and are having a greater impact on nesting success of small insectivorous birds. Mayfield (1977) found the Brown-headed Cowbird to be one of the most serious threats to survival of the endangered Kirtland's Warbler. The introduction of cowbirds into forest interior situations where they do not normally occur (Lowther and Johnston 1977) will have a detrimental effect on many of the neotropical insect-eating migrants that are restricted to the forest interior. The forest interior specialists are not adapted to cope with nest parasitism from the cowbird. Nearly all build open nests that are easily found by the cowbird, and most also raise only a single brood per year; thus, cowbird parasitism may destroy their entire annual production.

I am not saying that snags are bad in all interior situations, but I stress that if use of snags is promoted in the forest interior such snags should be clustered in a few areas rather than permitted to exist throughout a managed forest. Furthermore, when feasible, I recommend that tall snags that break the canopy be removed and shorter snags within the canopy be retained because cowbirds tend to select exposed perches.

Bear in mind that snags at or near a forest edge will frequently attract nesting Starlings, and the Starlings in turn compete with native hole-nesting species, especially flickers, Red-headed Woodpeckers, and bluebirds.

Reservoirs

One of the greatest disasters that can befall a forest bird community is the creation of a reservoir. In large sections of north central and northeastern United States the most extensive wooded areas are those in stream valleys. When such valleys are impounded for water supply, flood control, or recreation purposes, the more moist and generally most productive forest areas are destroyed, and many of the adjacent upland forest areas are fragmented to the point that they can no longer support the area-sensitive species of migratory birds. As an example, I would like to refer again to Rocky Gorge Reservoir near my home (fig. 6). Within the flooded basin of the reservoir, all of the lowland forest was destroyed. In addition, the remaining upland has been fragmented so

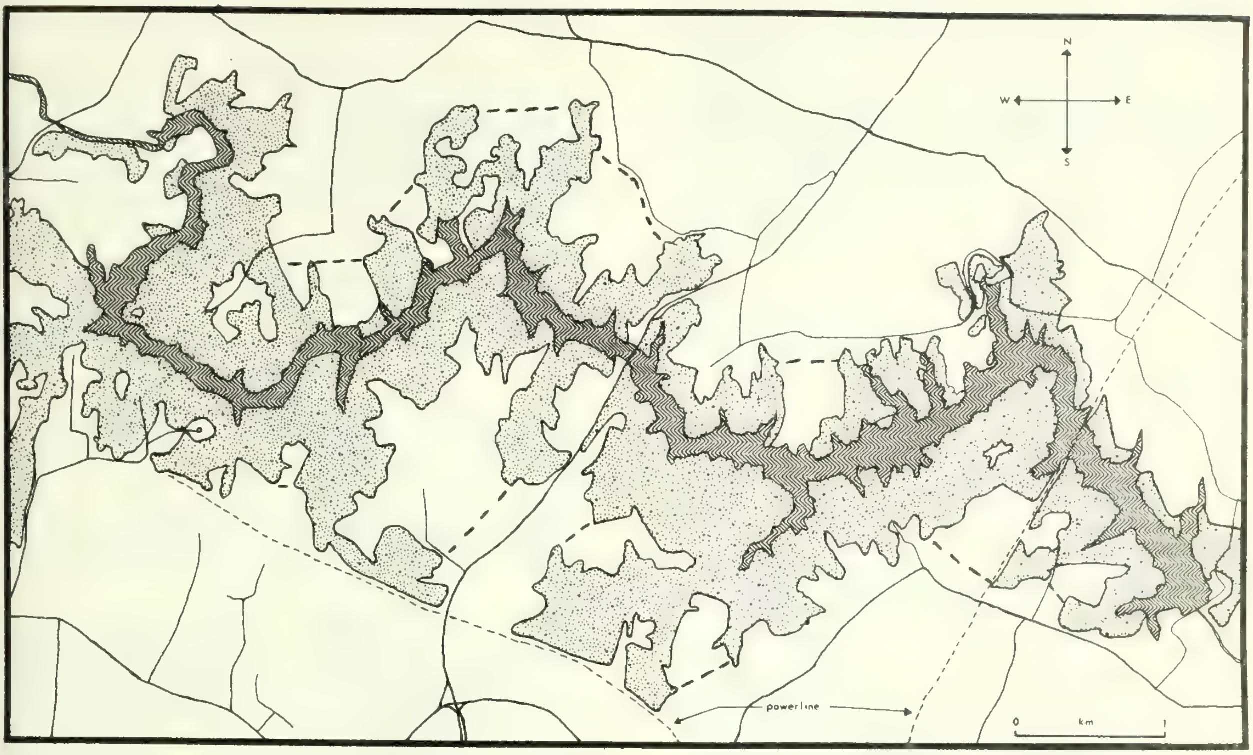


Figure 6.--Excessive fragmentation by Rocky Gorge Reservoir could have been prevented by planting forest within the dashed lines prior to destroying the original forest.

that now there is not a single point in the forest that is more than 300 meters from the forest edge. Although small numbers of many of the area-sensitive species still persist on these fragments, it is almost certain that these populations are doomed. The proximity of edge conditions throughout the area must inevitably lower reproductive rates of the present population, and there is no longer an adjacent mesic forest of higher productivity that can serve to offset losses in the peripheral population.

My reason for citing this example is that by means of proper long-range planning it would have been possible to protect or plant forest in strategically located areas adjacent to the impoundment before construction of the reservoir. If some of the areas marked with heavy dashed lines in figure 6 had been planted to forest before the area along the river was cut, several large areas of contiguous forest could have been retained, giving additional protection to the watershed and also providing refuge areas that could have served to perpetuate most of the avifauna typical of the original forest.

Corridors

One way to reduce the loss of area-sensitive species from forest fragments is by leaving (or planting) corridors that connect the fragment with a larger forested area (fig. 4f; see also MacClintock et al. 1977). The corridor concept has also been used successfully to bring woodland birds closer to residential areas during the non-breeding periods. Very few studies have documented effects of corridor width on bird populations, so no specific recommendations can be made now regarding the preferred width of such corridors or the extent that they are beneficial to certain species. Right now, I can only recommend retention of even a narrow corridor to prevent complete isolation of forest fragments. The corridor concept could also be carried too far. If a large number of small fragments were connected by corridors from the same source of repopulation, birds from a main forest might be enticed into fragmented woodlots where increased predation, competition from edge species, and other factors would prevent successful rearing of young (Whitcomb et al. 1979).

MANAGEMENT RECOMMENDATIONS

The following 16 recommendations stress steps that can be taken to retain the obligate forest-interior species in the breeding population. Nearly all of the edge species and those of the various seral stages will find suitable habitat regardless of the management techniques employed; these species are not so dependent upon large contiguous areas of similar habitat. Thus, most edge species of birds are not in danger of being eliminated from the species pool.

1. Avoid unnecessary fragmentation of forests (fig. 5e).

2. Manage in large blocks, or in such a way that small blocks are adjacent to more extensive forest.

3. In long-range plans designate tracts that will be mature or nearly mature at each stage in the management plan, and design normal management operations in such a way that repopulation of disturbed areas can proceed via wooded connections or over the smallest possible gaps in forest cover.

4. When possible, use a fairly uniform plan of rotation cutting (fig. 5a,b) so that the oldest sections at any time are adjacent to each other and the younger stages are adjacent to themselves, making the maximum usable area available to each bird species, no matter what its requirements.

5. Plan cooperatively with adjacent landowners so that maximum repopulation potential of those species that require extensive mature or near mature forest can be achieved.

6. In areas where mature forest is limited, consider preserving one or more strategically located mature tracts to serve as sources of avian repopulation.

7. In any management plan designate areas that are especially sensitive during any particular period of the year; and by posting or other means keep disturbance such as camping, hiking, picnicking, fishing, surveying, marking, or cutting to a minimum during the nesting season (May through early August).

8. When public use is part of a forest management plan, restrict activities to the edge of a sensitive area rather than permitting them to extend into its center.

9. Retain vegetational diversity to the extent feasible, because many studies have demonstrated a direct relation between vegetational diversity and avian diversity. It is not necessary to maintain high diversity in each separate management unit as long as there is diversity among different units. Grazing reduces diversity by removing or greatly reducing one or more of the important components of the forest vegetation.

10. Pending conclusion of more definitive studies on minimum habitat area requirements of various avian species, think in terms of 1,000 contiguous hectares (2,500 acres) of forest canopy as a desirable goal to preserve most or all of the avian species pool.

11. In smaller tracts (even down to 2 ha or less) it is beneficial to maintain the maximum contiguous woodland with the least amount of edge.

12. Management units that approach a square are much more effective in preserving forest-interior birds than are long, narrow ones--especially when managed tracts are small. The portions of a forest that are most beneficial to neotropical migrants are several hundred meters or more away from the forest edge.

13. Leave snags along forest edge or in patches in the forest interior, but not throughout the forest. In the forest interior select for preservation those snags that will not extend above the canopy of the nearly mature forest.

14. In any management plan consider the disruptive effects of other projects such as existing or proposed super highways, impoundments, transmission line corridors, or sewer lines (fig. 5d). Check with appropriate agencies on the timing of new construction, to avoid inadvertent loss of a critical area at the wrong time.

15. With reference to recommendation 14, provide mitigation planting as far in advance of the impending disturbance as possible (fig. 6).

16. If wooded fragments must be isolated from the forest proper, retain a connecting corridor, such as along a stream; or if a forest tract has already been separated, consider planting a corridor to reconnect it (fig. 5c,f).

ACKNOWLEDGMENTS

I thank Daniel Boone for preparation of the illustrations, Kathleen Hall for typing and formatting the manuscript, and Stanley Anderson, Danny Bystrak, Deanna Dawson, and Robert Whitcomb for constructive criticism of the manuscript.

APPENDIX

Scientific Names of Birds

Area-sensitive Species

Nonpasserines

Red-shouldered Hawk	Buteo lineatus
Broad-winged Hawk	Buteo platypterus
Yellow-billed Cuckoo	Coccyzus americanus
Whip-poor-will	Caprimulgus vociferus
Ruby-throated Hummingbird	Archilochus colubris
Pileated Woodpecker	Dryocopus pileatus

Flycatchers

Great Crested Flycatcher	Myiarchus crinitus
Acadian Flycatcher	Empidonax virescens
Eastern Wood Pewee	Contopus virens

Thrushes

Wood Thrush	Hylocichla mustelina
Veery	Catharus fuscescens

Vireos

Yellow-throated Vireo	Vireo flavifrons
Red-eyed Vireo	Vireo olivaceus

Wood Warblers

Black-and-white Warbler	Mniotilta varia
Prothonotary Warbler	Protonotaria citrea
Worm-eating Warbler	Helmitheros vermivorus
Northern Parula Warbler	Parula americana
Pine Warbler	Dendroica pinus
Ovenbird	Seiurus aurocapillus
Louisiana Waterthrush	Seiurus motacilla
Kentucky Warbler	Oporornis formosus
Hooded Warbler	Wilsonia citrina
American Redstart	Setophaga ruticilla

Tanagers

Scarlet Tanager	Piranga olivacea
Summer Tanager	Piranga rubra

Other Species Mentioned

Ruffed Grouse	Bonasa umbellus
Red-bellied Woodpecker	Melanerpes carolinus
Red-headed Woodpecker	Melanerpes erythrocephalus
Hairy Woodpecker	Picoides villosus
Blue Jay	Cyanocitta cristata
Tufted Titmouse	Parus bicolor
White-breasted Nuthatch	Sitta carolinensis
House Wren	Troglodytes aedon
Carolina Wren	Thryothorus ludovicianus
Starling	Sturnus vulgaris
Kirtland's Warbler	Dendroica kirtlandii
Prairie Warbler	Dendroica discolor
Brown-headed Cowbird	Molothrus ater
Orchard Oriole	Icterus spurius
Blue Grosbeak	Guiraca caerulea

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Thursday, January 25

SPECIALIZED HABITAT CONSIDERATIONS FOR NONGAME BIRDS

Moderator: Charles J. Griffith
National Wildlife Federation

SNAG MANAGEMENT

Keith E. Evans and Richard N. Conner[1]

Abstract.--Thirty-six of the 85 North American cavity nesting bird species occur in the north-central and northeastern forests. Species richness and density are influenced by the quality and quantity of available snags. Snag abundance is influenced by many land use options including timber operations. We have calculated the snag needs for 9 primary excavators and have related these needs to management options.

Only recently have wildlifers expressed great concern for animals that depend on the dead and dying tree (snag) component of the forest--especially for avifauna classified as cavity nesters. These birds evolved in unmanaged forest stands where snags occur naturally and are dependent on snags for at least a portion of their life requirements. Since 90 percent of the trees present in an upland hardwoods stand at age 20 will die during the next 60 years (Gingrich 1971), there are many standing dead and dying trees found in naturally developing forests.

Each resource discipline views the snag component of forests differently. Foresters know that growth can be increased and mortality decreased by periodically thinning forest stands. Thinning a forest selects against subdominant, low-vigor, silviculturally defective and low-quality trees--trees that have the highest potential to become suitable snags. Snags and potential snags are often referred to as "ugly" by the landscape architects, and "hazards" by the forest protection and safety divisions. Although these concerns are occasionally valid, across the board condemnation is unwarranted.

The objectives of this paper are to (1) identify bird species that depend on snags, (2) discuss the specialized requirements of these bird species, (3) relate snag attributes to management options for bird species, (4) calculate the number of snags required, and (5) make management recommendations.

EXPLANATION OF TERMS

Snag

A snag is a standing dead or partially dead tree. Snag attributes and the requirements of birds depending on these attributes vary greatly. Generally, the value of a snag increases as its size increases. Snags less than 10 cm d.b.h. and/or less than 2 m tall have little value for feeding and nesting birds. The snag characteristics of primary interest are natural cavities and a condition that makes a snag suitable for cavity excavation (fig. 1).

Hard and Soft Snags

The classification of a snag as "hard" or "soft" is somewhat subjective. Generally, hard snags are dead or partially dead trees with at least some limbs remaining and with fairly sound wood. Soft snags are in advance stages of decomposition and rarely have limbs.

Natural Cavity

A space hollowed out of a tree by a force other than a bird. These holes are commonly created by fungal rot, insects, fire, or the breakage of the wood fiber.

Primary Excavator

A bird species that excavates or hollows out a space within a snag for nesting or roosting. The woodpeckers are the major group of primary excavators. Their habit of excavating partial or complete cavities in excess of their needs provides the major supply of cavities for secondary users.

Secondary Users

A bird species that nests or roosts in a natural cavity or a cavity excavated by a primary excavator. Certain species, such as the black-capped chickadee, can be both a primary excavator and secondary user.

Bark Cavity

A space created by loose bark. These spaces are used by insects, reptiles, amphibians, mammals, and birds, e.g., brown creepers

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[1] Principal Wildlife Biolgoist, North Central Forest Experiment Station, Columbia, MO; and Research Wildlife Biologist, Southern Forest Experiment Station, Nacogdoches, TX, respectively.

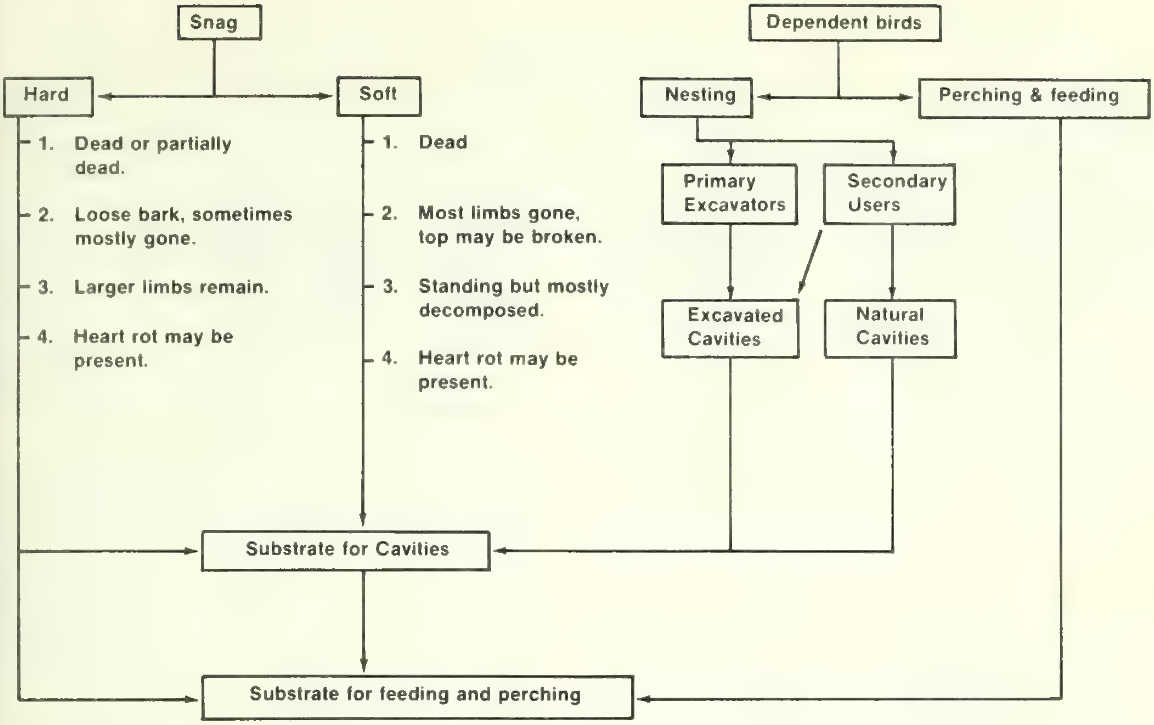
Snag
Hard
Soft
1. Dead or partially dead.
2. Loose bark, sometimes mostly gone.
3. Larger limbs remain.
4. Heart rot may be present.
1. Dead
2. Most limbs gone, top may be broken.
3. Standing but mostly decomposed.
4. Heart rot may be present.
Dependent birds
Nesting
Perching & feeding
Primary Excavators
Secondary Users
Excavated Cavities
Natural Cavities
Substrate for Cavities
Substrate for feeding and perching

Figure 1.--*Diagram of snag types and generalized use patterns.*

Usually formed after a tree or tree limb has died.

Woodpecker Territories

Disagreement exists in the literature as to what type of territories different species of woodpeckers defend. Lawrence (1966) reported that several species in Ontario defended nesting and mating territories (type B) (Nice 1941). Brenowitz (1978) and others have noted that sizes of defended areas for many species varied within species depending on the species intruding; thus, a pair may defend nesting, mating, and foraging territory (type A) when interacting with one species, and Type B territory when interacting with another.

The values used for sizes of woodpecker territories in this paper include the area used by pairs for nesting, mating, and foraging--a type A territory using the code developed by Nice (1941). Also, for some of the woodpecker species examined in this paper, the word "range" may be more scientifically correct than the word "territory".

DEPENDENT BIRD SPECIES

Some 85 species of North American birds nest and/or roost in dead or deteriorating trees (Scott *et al.* 1977). These species either excavate cavities, use cavities created by decay or breakage, or use cavities constructed by other species. The snag-dependent species--hole nesters--make up 20 percent of the bird species encountered on the breeding bird survey routes in Missouri (Evans and Dawson 1976). Most of these species are insectivorous, and may help control insect populations that damage timber. The winter bird populations in the northeast consist of an even higher percentage of cavity-dependent birds. Bock and Lepthien (1974) found that the average Christmas bird count for the northeast contained 40 species of birds. The list of birds we are considering in this paper (table 1) contains 26 species that winter in the area.

Although the hole nesters have some common characteristics and requirements, they are a diverse group. They range in size from 11-1500 grams and utilize territories from less than 1 ha to over 140 ha (table 1). Management options must be equally diverse. We have simplified the management proposals by (1) concentrating our comments on the primary excavators, and (2) considering only the snag component of their life requirements. If suitable numbers and sizes of snags are provided for primary excavators, the snag requirements of secondary users hopefully will be attained.

SUITABILITY OF HARDWOOD AND PINE SNAGS AS CAVITY SITES

Recently, the importance of snags in forests and lumbered areas has become widely recognized

Table 1.--*Characteristics of cavity-nesting birds of the northeastern United States*

Species[1]	Snag use				Hard snags	Soft snags	Secondary	Optimum d.b.h. (cm)				N. hardwood	Lowland hardwood	Aspen-birch	Oak	Pine	Upland conifer	Lowland conifer	Hole size	Box size			Territory size	Body weight
	Feed	Perch	Nest	Roost				10	20	30	50+									Length	Width	Height		
																			- - -	cm	- - -		*ha*	*g*
Wood duck			X				X				X		X						10	25	25	60		
Common goldeneye			X				X				X							X	10	30	30	60		
Hooded merganser			X				X				X		X					X	10	25	25	60		
Common merganser			X				X				X							X	12	25	25	90		
Turkey vulture		X	X				X				X	X	X	X	X	X								1500
Peregrine falcon		X	X				X				X	X		X			X							
Merlin		X	X				X				X			X	X		X							
American kestrel		X	X				X			X		X	X	X	X	X	X	X	8	25	25	40	142	115
Barn owl		X	X	X			X				X	X	X		X	X			13	33	38	40		500
Screech owl		X	X	X			X			X		X	X	X	X	X	X	X	8	20	20	30		178
Barred owl		X	X	X			X				X	X	X		X				20	33	38	40		800
Boreal owl		X	X	X			X			X							X	X	7					
Saw-whet owl		X	X	X			X			X				X	X	X	X		6	15	15	30	40	90
Chimney swift			X	X			X				X	X	X	X	X	X	X	X		Chimneys				
Common flicker	X	X	X	X	X	X	X			X		X	X	X	X				7	18	18	40	16	134
Pileated woodpecker	X	X	X	X	X	X					X	X	X		X	X			10				70	230
Red-bellied woodpecker	X	X	X	X	X	X				X		X	X		X	X							6	62
Red-headed woodpecker	X	X	X	X	X	X					X	X		X	X				5				4	66
Yellow-bellied sapsucker	X	X	X	X	X	X				X			X	X	X	X	X						4	47
Hairy woodpecker	X	X	X	X	X	X				X		X	X	X	X	X	X		4	15	15	35	8	44
Downy woodpecker	X	X	X	X		X			X			X	X	X	X	X	X	X	3	10	10	25	4	27
Black-backed three-toed woodpecker	X	X	X	X	X	X				X							X	X					30	
Northern three-toed woodpecker	X	X	X	X	X	X				X							X	X					30	
Great crested flycatcher		X	X				X			X		X	X	X	X				5	15	15	25		34
Tree swallow			X				X			X			X		X			X	4	12	12	15		20
Purple martin			X	X			X			X		X		X	X	X			6	15	15	15	3	43
Black-capped chickadee			X			X		X				X		X	X	X	X		3	10	10	25	1.5	11
Boreal chickadee			X			X		X						X			X	X	3	10	10	25		
Tufted titmouse			X	X			X			X			X		X				3	10	10	25		23
White-breasted nuthatch	X		X	X			X			X		X	X	X	X	X	X	X	3	10	10	25	0.8	20
Red-breasted nuthatch	X		X	X		X	X			X							X	X	3	10	10	25		
Brown creeper	X		X	X			X			X		X				X	X	X				25		9
House wren			X	X			X			X			X	X	X	X	X	X	3	10	10	20	0.5	11
Winter wren			X				X		X							X	X		3					9
Eastern bluebird		X	X	X			X		X			X		X	X				4	12	12	20	1.0	30
Prothonotary warbler			X				X		X				X										1.5	16

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[1] Scientific names in Appendix A.

(McClelland and Frissell 1975, DeGraaf 1978, Scott 1978). Techniques to calculate the number of snags required by individual species appeared in Balda (1975), Bull and Meslow (1977), and Thomas *et al.* (1976). The snags provided should be suitable for nest cavity excavation. To be suitable for cavity sites, snags should be large enough in diameter and have decayed heartwood at a height appropriate for a bird species to excavate a nest cavity (table 2). Primary excavators prefer trees with heart rots because the soft, rotted wood facilitates cavity excavation (Conner *et al.* 1976).

Several states of decay are suitable for cavity excavation, but some are better "quality" for nest sites than others. The best quality nest site is a live tree with a "top rot", decayed heartwood in the upper trunk or main limbs of the tree. Such trees have a firm sapwood which is highly effective as a defense against predators (Kilham 1971, Conner 1977b). Top-rotted trees are often used by woodpeckers when nesting in hardwoods (Conner *et al.* 1975).

A less defensible nest tree is one having both heart and sap rotting fungi present at the site of the nest cavity. Sap rots infect the sapwood of trees, softening it and killing the affected tree or limb. If the sapwood is soft, predators can easily enlarge the cavity entrance tube and prey on young or adults. However, certain species that are not strong excavators (e.g., downy woodpeckers[2/]) may be partially dependent on snags with both heart and sap rots when they nest in trees with "hard" wood, e.g., oaks, hickories, etc. (Conner 1978).

Beetle-killed pines are an additional type of snag available for cavity nesters. These snags are often quite soft because invading beetles and broken branches have exposed most of the wood to fungal attack. Due to extensive decay in both sapwood and heartwood these snags often do not stand for long periods of time.

The least desirable nest tree condition occurs when only the sapwood of a snag is rotted. When a nest cavity is excavated into just the sapwood, the cavity is quite vulnerable to predation, and possibly temperature extremes. The thickness of wood between the cavity and the outside of the tree is typically minimal in such cavities. Thus, the insulation value of the cavity (Kendeigh 1961) may be greatly reduced.

Possible Indicators of Suitable Snags

Snags with potential nest sites have many indicators (Conner 1978). Fungal conks, rotting dead branch stubs, old wounds or scars, existing woodpecker cavities, and dead portions on trees are some obvious characteristics indicating the possible presence of a suitable substrate. Coring snags with an increment borer and/or culturing fungi from these cores are more difficult methods to determine suitability of snags (Conner *et al.* 1976).

SNAGS AS FORAGING SUBSTRATES

In addition to their importance as nest sites, snags are used extensively by many birds as foraging sites. The surface of a live tree is a complex habitat. Crevices formed by the bark provide sites for spiders, ants, moths, and other invertebrates to hide. These invertebrates are the mainstay diet of the bark gleaning birds.

As a tree dies, it is invaded by many additional insects. Noteworthy of these are the numerous species of bark beetles that feed in the cambium of the tree. Larvae, pupae, and adults are a major food item of many woodpeckers (Otvos 1965). Woodpeckers extract the larvae of these insects after pecking small holes through the bark. Later in the beetles' life cycle woodpeckers need to make excavations to gain access to larvae that have gnawed a tunnel into the sapwood to pupate.

Additional prey are found in the heartwood of the snags. Carpenter ant (*Camponotus* spp.) and termite (Isoptera) colonies are rich food supplies for woodpeckers strong enough to penetrate the tree shell protecting the caverns (Conner 1977a).

CALCULATION, SIZES, AND DISTRIBUTION OF SNAGS REQUIRED

In this paper we have used the formula developed by the U.S. Forest Service (Bull and Meslow 1977) to calculate the number of snags required by species:

$$Y = A \times B \times C$$

Where: Y = number of suitable-sized snags required standing at any given time per 40 ha (100 acres).
A = maximum bird species density per 40 ha (100 acres).
B = number of snags used annually (or for a specific season).
C = snag reserve, some snags will fall and need replacement, some available snags will be unsuitable for cavity excavation, and some snags will be used as feeding but not nesting sites.

[2/] Scientific names in Appendix.

Table 2.--*References and characteristics of territories and nest trees needed to calculate snag densities for 9 species of woodpeckers common to the northeastern United States*

Species	When using territory	Territory size		Minimum no. of snags used	Average d.b.h. of nest trees		Average height of nest trees		Maximum pairs per:		Literature
		ha	*(ac)*		*cm*	*(in)*	*m*	*(ft)*	100 ha	(100 ac)	
Downy woodpecker	All year	4	(10)	4	20	(8)	6	(20)	25	(10)	Allen (1928), Kilham (1962), Lawrence (1966), Conner *et al.* (1975, & unpublished data), Bull (1978)
Hairy woodpecker	All year	8	(20)	4	30	(12)	9	(30)	12.5	(5)	Kingsbury (1932), Kilham (1960, 1966, 1968), Lawrence (1966), Conner *et al.* (1975)
Pileated woodpecker	All year	70	(175)	4	55	(22)	18	(60)	1.4	.6	Becker (1942), Tanner (1942), Hoyt (1957), Kilham (1959, 1976), Conner *et al.* (1975), Bull (1978)
Common flicker	Breeding	16	(40)	2	37	(15)	9	(30)	6.3	(2.5)	Lawrence (1966), Conner *et al.* (1975), Bull (1978)
Red-bellied woodpecker	All year	6	(15)	4	45	(18)	12	(40)	16.7	(6.7)	Tanner (1942), Kilham (1958a), Boone (1963), Stickel (1964), Reller (1972), Conner (1973), Jackson (1976)
Red-headed woodpecker	Breeding	4	(10)	2	50	(20)	12	(40)	25	(10)	Kilham (1958b), Reller (1972), Conner (1976, & unpublished data), Jackson (1976)
	Winter	.1	(.3)	1	50	(20)	12	(40)	1000	(333)	
Black-backed three-toed woodpecker	All year	30	(75)	4	38	(15)	9	(30)	3.3	(1.3)	Bent (1939), Short (1974), Bull (1978),(Territory size assumed to be same as northern three-toed woodpecker)
Northern three-toed woodpecker	All year	30	(75)	4	35	(14)	9	(30)	3.3	(1.3)	Laing and Taverner (1929), Bent (1939), Gibbon (1966), Bull (1978), Thomas *et al.* (Unpublished manuscript)
Yellow-bellied sapsucker	Breeding	4	(10)	1	30	(12)	9	(30)	2.5	(10)	Howell (1952), Lawrence (1966), Kilham (1971, Personal communication), Bull (1978), Thomas *et al.* (Unpublished manuscript)

Maximum Density

A maximum population density must be used in order to determine what number of snags are needed to support this density. Territory sizes and densities of pairs listed in table 2 are based on values found in the literature. In a few cases assumptions and adjustments were needed. Due to a lack of information, the territory size of black-backed three-toed woodpeckers was assumed to be similar to northern three-toed woodpeckers. Since the black-backed three-toed woodpecker is larger than the northern three-toed, it probably required a larger territory; thus our assumption may provide slightly more snags than the bird actually requires as a maximum.

Many population densities have been reported for pileated woodpeckers; the highest being one pair per 106 acres (Tanner 1942). However, this value was measured in southern United States where food may be more abundant for a longer portion of the year than in northeastern United States. Thus, we adjusted territory size to one pair per 175 acres to obtain what is probably a more realistic maximum for the Northeast. This value, 175 acres or 70 ha, is also the range size reported for pileateds by Kilham (1976).

Number of Snags Used Annually

Woodpeckers use cavities in trees for nesting and roosting. If all conditions are favorable, a pair of woodpeckers uses only one nest cavity annually. However, often predators and competitors cause a cavity to be unsuitable (Allen 1928, Balda 1975).

Ideally, only two roost cavities are needed annually. Field observations, however, indicate that several roost cavities per individual bird may be needed as both sexes frequently move to different roost cavities (Allen 1928, Hoyt 1957, Stickel 1964). Natural selection may have favored this behavior to reduce losses of roosting woodpeckers to nocturnal predators.

After fledging, young woodpeckers of most species require roost cavities, which adds at least one more cavity to the annual requirement. Thus, for most woodpeckers, pairs require a minimum of 4 suitable cavity trees (or snags) each year (table 2). Annual cavity requirements are different for the migratory woodpeckers, common flickers, yellow-bellied sapsuckers, and red-headed woodpeckers, as they need winter roosting sites in a different area than nesting sites.

Reserve of Snags

It is difficult, if not impossible to determine the percentage of snags in a forest that are suitable for cavity excavation. Thomas *et al.* (1976) reported that only one snag out of 17 in Oregon contained a nest cavity. This however, does not preclude the possibility that some of the 16 unused snags were suitable for cavity excavation. Availability of food, as suggested by McClelland (1979), may be a limiting factor that reduces woodpecker densities in the Pacific Northwest. Low population densities of cavity excavators and/or spacing of snags may cause some suitable snags to be unused. Variations in the percentage of snags that are suitable for cavity excavation will be influenced by site characteristics, geographical location, and the species of the tree involved. In addition, a reserve of snags is needed to replace cavity trees lost each year.

We have used the value 10 as an estimate of the number of snags needed to provide cavity substrate for each cavity required by a pair of woodpeckers. This value includes a margin for unusable snags, a reserve of snags for replacements, feeding habitat, and a supply for secondary users.

Snags Required to Support Percentages of Population Maximums

Once the number of snags required to support maximum densities of woodpecker species is determined (Y in the formula), various percentages of these values can be used to estimate the number of snags required to support percentages of population maximums (table 3). These values are estimates based on the best information currently available. If future research provides more accurate base data, the estimates of snags required should be recalculated and the new values used for habitat management projects in the field.

Snag Height and DBH

Thomas *et al.* (1976) and Bull (1978) mentioned the use of minimum heights and DBH's of snags when providing snags for cavity nesters. We discourage the use of minimum values.

The DBHs and heights of species' nest trees tend to be normally distributed, most observation falling near the mean and few at the "tails" of a normal distribution curve. Natural selection favors individuals nesting in trees with d.b.h.'s and heights close to the mean, and often reduces productivity of pairs nesting in trees with d.b.h.'s and heights at the minimum or maximum extremes.

If trees are too small in diameter, crowding may reduce the number of offspring that can fit in a cavity. Studies in Europe indicated that some cavity nesting species increase their clutch size with increases in nest box sizes (Karlsson and Nilsson 1977). This relationship may also exist in species nesting in natural or

Table 3.-- *Recommended numbers of snags to maintain selected densities of woodpecker populations in northeastern United States*

Species	Probable optimum d.b.h. ranges of nest trees		Optimum ranges of nest tree heights		Snags needed per 40 ha (100 acres) to maintain listed percentages of population maximums				
					Good		Fair		Poor
					100	80	60	40	20
	cm	*(in)*	*m*	*(ft)*	- - - - - - *Number* - - - - - - -				
Downy woodpecker	15-25	(6-10)	3-9	(10-30)	400	320	240	160	80
Hairy woodpecker	25-35	(10-14)	6-12	(20-40)	200	160	120	80	40
Pileated woodpecker	45-65	(18-26)	12-21	(40-70)	24	19	14	10	5
Common flicker	30-44	(12-18)	6-12	(20-40)	[1]50	40	30	20	10
Red-bellied woodpecker	36-53	(14-22)	9-15	(30-50)	270	220	160	110	55
Red-headed woodpecker	40-60	(16-24)	9-21	(30-70)	[1]200	160	120	80	40
					[2]3,330	2,660	2,000	1,330	670
Black-backed three-toed woodpecker	30-46	(12-18)	6-12	(20-40)	52	42	31	21	10
Northern three-toed woodpecker	30-40	(12-16)	6-12	(20-40)	52	42	31	21	10
Yellow-bellied sapsucker	25-35	(10-14)	6-12	(20-40)	[1]100	80	60	40	20

[1] Breeding season requirements.

[2] Wintering habitat requirements.

excavated cavities. As crowding increases, juvenile cavity nesters may kill siblings (Kilham[3]). If nest trees provided are only of minimum height, predators may seriously reduce the reproductive success of populations using such snags (Holcomb and Twiest 1968, Dennis 1969). Thus, if we provide only minimum sized snags (DBH and height) we may eliminate a species by not providing the size of nest tree that natural selection favors.

Snags provided for woodpecker species should be within the appropriate DBH and height ranges required by the species (table 3), preferably, as close as possible to the mean DBH's and heights listed in table 2. By providing the average sized snags, the probability of meeting species requirements can be maximized.

Distribution of Snags Provided

When snags are provided for cavity nesters, snag distribution must not prohibit or reduce the chance of snags being used. Thus, a uniform distribution of snags may be the best in a forest situation. This distribution optimum may not always be possible, especially during early regeneration stages of clearcuts. In such cases, a belt of "old growth" along water influence zones or a good distribution of small clumps of older trees with abundant snags within younger forest stands would be of great value to cavity nesters.

MANAGEMENT OPTIONS

One concept should dominate designs of management programs--each wildlife species has an intrinsic value in the perpetuation of natural ecosystems. Therefore, effort should be directed toward achieving or maintaining self-sustaining population levels of all native species. Many current land use patterns in eastern forests maintain structural complexity and support a correspondingly diverse avifauna. Most breeding bird species in this area have a wide geographical range, are mobile, and in no current danger of being reduced to less than a self-sustaining population. Some species, especially those that tolerate only a narrow range of habitat variability or require a specialized habitat component, need a more specialized management program. Cavity nesters fit into this category.

Four broad management options are open to the forest manager, each with its own implications to avian habitat values. These options are exploitation, even-aged management, unevenaged management and preservation. Exploitation involves no silvicultural system. The silvicultural systems which might be employed to implement the even-aged management option include shelterwood, seedtree, and clearcutting systems. The selection system--either single tree or group selection--would be used in uneven-aged management. The preservation option includes active protection of a stand or the no-management, no-use, leave alone option. These were discussed in greater detail by Zeedyk and Evans (1975). How these options might affect nongame birds are as many and as varied as the bird species and forest types involved. The preservation option probably provides the best opportunity for an abundance of snags and corresponding populations of snag-dependent species. We are not recommending the preservation option for any large area because of the other values of a well-managed forest and the negative impact on the many bird species that require an early successional stage.

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[3] Personal communication.

For the production of high quality sawtimber and veneer trees in the oak-hickory forests, even-aged management is recommended (Sander 1977, Roach and Gingrich 1968). This objective can best be attained with clearcutting or some form of shelterwood. The time required to grow trees to a given diameter can be greatly reduced and the forest yield substantially increased if thinnings are initiated early in the life of a stand (Sander 1977). When management prescriptions call for thinning to begin at age 20 and occur at 10-year intervals, the effect on cavity-nesting species could be disastrous. Gingrich (1971) reported that at age 20 an unthinned upland hardwood stand will contain from 3,400 to 6,200 trees per hectare, and during the nest 60 years, without thinning, 90 percent of these will die. These dead and dying trees are essential habitat components for at least 26 cavity-nesting species of birds in the oak-hickory forest (Hardin and Evans 1977).

Condition of currently available forest stands and rotation age plays an important role in the management of hole nesting species. Over 50 percent of the 116 billion trees in the northeast are less than 5 cm (3 in) d.b.h. (U.S. Department of Agriculture Forest Service 1977). Nearly all of the primary cavity excavations require a snag of 23 cm (9 in) d.b.h. for their nesting hole. Only 8 percent of the hardwood trees in the northeast are 23 cm d.b.h. or larger (table 4). The situation is even worse for the softwoods of the northeast--less than 6 percent are over 23 cm (9 in) d.b.h. Out of 116 billion trees in the northeast 8 billion are 23 cm d.b.h. or greater. Observing the number of live trees per unit area provided a base for snag management considerations (table 5). This illustrates two concerns, (1) only a small percentage of the living trees are large enough to provide suitable cavity substrate and (2) in a managed forest these large trees are not likely to be left for snags.

Table 4.--*Percent of live hardwoods by d.b.h. classes in various regions*[1]

D.b.h.		North	Minnesota	Missouri
in	*cm*	- - - *Percent*	- - -	
1	2.5	[2]100	100	100
3	7.6	48	48	39
5	12.7	25	26	19
7	17.8	14	12	11
9	22.9	8	5	6
11	27.9	5	2	4
13	33.0	2	1	2
15	38.1	1	0.6	1
17	43.2	0.1	0.3	0.5
19	48.3	0.003	0.13	0.3
21	53.3	0.002	0.06	0.14

[1] Source: USDA Forest Service (1977).

[2] Percent of trees of this d.b.h. and larger.

Table 5.--*Number of live trees per 40 ha (100 acres) on commercial timberland in the northeast*[1]

D.b.h.		Live trees per 40 ha (100 acres)	
		Hardwood	Softwood
in	*cm*	- - *Number*	- -
1	2.5	[2]49,062	19,061
3	7.6	23,453	9,741
5	12.7	12,347	4,832
7	17.8	6,726	2,306
9	22.9	3,676	1,076
11	27.9	1,997	499
13	33.0	1,099	235
15	38.1	591	112
17	43.2	316	54
19	48.3	171	26
21	53.3	93	13
29	73.7	11	1

[1] Source: USDA Forest Service (1977).

[2] Number of trees of this d.b.h. and larger.

We won't discuss the wide variety of generalized snag management options that have previously been discussed (Conner 1978, Evans 1978). The one obvious factor is that under an even-aged management system, most of the stands will be too young to provide adequate size snags; we need to protect some areas from regeneration cuts. Zeedyk and Evans (1975) recommended leaving a 0.1 ha clump of trees within each 2 ha of regeneration (0.25 acre within each 5 acres of harvest area). Although each area would be different, this would provide between 830 (site index 75) and 1,210 (site index 55) trees left standing after clearcutting per 40 ha (100 acres). For upland hardwood stands the dominant trees on site index 55, at age 80, will average about 30 cm (12 in) d.b.h., whereas the dominant trees on site index 75, at age 80, will average 45 cm (18 in) d.b.h. (Gingrich 1971).

Although additional research would be required to evaluate this management proposal, a 5 percent trade-off in timber growing space would probably provide some of the smaller cavity nesting species adequate habitat during later stages of timber regeneration. This would not be true for larger woodpeckers such as the pileated, and possibly hairy woodpeckers which require more extensive areas of continuous forest. The arrangement of these clumps could be somewhat flexible. Combining 4 of these clumps together could provide a 0.4 ha (1 ac) mature forest in each 8 ha (20 ac) of young (regenerating) timber. These islands would provide limited foraging and nesting sites immediately following clearcutting and be of value for a long period of time.

Each stand would probably have a drainage system that needed to be protected or a partially inaccessable area. These areas could also be left uncut to provide mature forest area for forest cavity nesters with large home range requirements. We recommend that an uncut area of of 20 times the stream width, not to exceed 50 m, be left on both sides of water courses. These buffer strips will provide habitat for both game and nongame species in addition to greatly reducing erosion and stream siltation. The resulting canopy cover over streams will also prevent stream warming which negatively affects desired fish species.

THE VALUE OF MATURE FORESTS AND INSECTIVOROUS BIRDS

Economic advantages of providing areas with mature forest habitat for cavity nesters may at first seem remote. However, evidence suggests that long term advantages may exist. Most cavity nesters are insectivorous and many studies have demonstrated their effectiveness in reducing populations of insect pests that attack and destroy trees (Baldwin 1958, Knight 1958, Otvos 1965, Shook and Baldwin 1970, Koplin 1972). When woodpeckers forage on insect infested trees there are secondary benefits. Typically, they chip bark off while foraging which increases the effectiveness of insects that parisitize the insects that are attacking the tree (Otvos 1965).

In order for insectivorous birds to buffer insect epidemics, they must be maintained at sufficient population densities. Providing enough snags to maintain bird populations in mature forest habitat is crucial, especially for primary excavators.

Insectivorous birds that are secondary users of nest cavities will often nest in artificial nest boxes. Providing nest boxes for such birds can increase avian population densities greatly while concurrently decreasing densities of insects (Bruns 1960, Tichy 1963, Campbell 1968). Table 1 provides nest box and entrance hole dimensions for selected species.

If insect outbreaks occur when insectivorous bird populations are at sufficient densities, the birds can concentrate in areas of outbreaks and buffer, contain, or possible eliminate the insect infestation, thus possibly reducing economic losses. Concentration of insectivorous birds at insect infestation does occur and has been documented (Blackford 1955, Yeager 1955, Morris *et al.* 1958, Koplin 1969).

Additional benefits can be derived if natural predators are used to control insect pests. Biological control may eliminate or reduce the expense, "pesticide resistance" problems, and environmental dangers of pesticide applications.

Recommendations

1. Manage for maximum feasible rotation age.
2. Consider old growth a high priority optio Select stands for deferred cutting as earl as possible--age 20 is optimum.
3. Leave a 0.1 ha clump permanently uncut in each 2 ha of regeneration cut.
4. Discontinue removal of dead, dying, and decayed trees for use as materials or firewood in areas where nest cavity sites are limited.
5. Consider management techniques such as pr viding artificial nest boxes and boring holes in suitable sized trees when cavity availability is limited.
6. Consider leaving permanent uncut buffer strips on both sides of streams.

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APPENDIX

Wood duck- - - - - - - - - - - - - - - - -*Aix sponsa*
Common goldeneye - - - - - - - -*Bucephala clangula*
Hooded merganser - - - - - *Lophodytes cucullatus*
Common merganser - - - - - - - - -*Mergus merganser*
Turkey vulture - - - - - - - - - - -*Cathartes aura*
Peregrine falcon - - - - - - - - -*Falco peregrinus*
Merlin - - - - - - - - - - - - - - *Falco columbarius*
American kestrel - - - - - - - - -*Falco sparverius*
Barn owl - - - - - - - - - - - - - - - - - *Tyto alba*
Screech owl- - - - - - - - - - - - - - - *Otus asio*
Barred owl - - - - - - - - - - - - - - - *Strix varia*
Boreal owl - - - - - - - - - - - *Aegolius funereus*
Saw-whet owl - - - - - - - - - - *Aegolius acadicus*
Chimney swift- - - - - - - - - - *Chaetura pelagica*
Common flicker - - - - - - - - - -*Colaptes auratus*
Pileated woodpecker- - - - - -*Dryocopus pileatus*
Red-bellied woodpecker - - -*Melanerpes carolinus*
Red-headed woodpecker-*Melanerpes erythrocephalus*
Yellow-bellied sapsucker - - -*Sphyrapicus varius*
Hairy woodpecker - - - - - - - - *Picoides villosus*
Downy woodpecker - - - - - *Dendrocopus pubescens*
Black-backed three-toed- - -
    woodpecker- - - - - - - - - *Picoides arcticus*
Northern three-toed
    woodpecker- - - - - - - -*Picoides tridactylus*
Great crested flycatcher - - -*Myiarchus crinitus*
Tree swallow - - - - - - - - - - *Iridoprocne bicolor*
Purple martin- - - - - - - - - - - - - -*Progne subis*
Black-capped chickadee - - - -*Parus atricapillus*
Boreal chickadee - - - - - - - - -*Parus hudsonicus*
Tufted titmouse- - - - - - - - - - - *Parus bicolor*
White-breasted nuthatch- - - -*Sitta carolinensis*
Red-breasted nuthatch- - - - - -*Sitta canadensis*
Brown creeper- - - - - - - - - -*Certhia familiaris*
House wren - - - - - - - - - - - *Troglodytes aedon*
Winter wren- - - - - - - *Troglodytes troglodytes*
Eastern bluebird - - - - - - - - - - *Sialia sialis*
Prothonotary warbler - - - - *Protonotaria citrea*

RAPTOR MANAGEMENT AND REHABILITATION

Patrick T. Redig [1]

The medical and surgical treatment of injured raptors has potential for significantly mitigating the effects of unnatural mortality among certain species, notably the Bald Eagle and Peregrine Falcon. Since 1972 over 1200 raptors have been treated in our facility, 101 of which were eagles and 15 were Peregrine Falcons. The relevance of rehabilitation as a management tool is discussed in the context of the overall status of raptor management.

The management of raptors has become a subject of considerable widespread interest only since about 1966 (Fyfe, 1976). Since then there has been a great deal of research performed, primarily through academic institutions. Such research has been only partially related to management and has most frequently been very local in geographic scope and narrow in terms of subject scope (e.g., behavior at the nest, nest site habitat, food habits during the breeding season). Fuller (1978) has made the observation that the majority of raptor field studies have been conducted on the plains of the Western United States. With the exception of a few locally studied areas such as the Bald Eagles in the Great Lakes States, and studies done in Florida, Ohio, and Pennsylvania there is a real paucity of literature pertaining to eastern raptors. These patterns possibly relate to those general difficulties of studying the thinly distributed populations of very mobile, wide ranging predators. In the eastern forest,observations (other than at nest sites), are very difficult; thus more studies have been done in open areas. The scarcity of research leaves little for the manager to work with. However, the raptors respond to the same management principles as those already researched and in use for species that have been managed for forty or more years (Hamerstrom, 1974). Thus the obvious conclusion of habitat preservation as a key item in the survival formula of raptors is easily achieved. For the practical purposes of developing management programs a breakdown into specific areas of effort within the framework of habitat preservation is necessary. Of the many approaches that may be taken, there are four facets which have been experimented with to considerable degree in the management of raptors during the 1970's and these are: 1) identification and protection of nesting sites, 2) providing and protecting uncontaminated food supplies, 3) augmenting production through providing additional nesting sites where a shortage of these is identified as a limiting factor, captive rearing and release of youngsters through fostering or hacking, and manipulation of clutches at either the egg or nestling stage, and 4) reducing mortality in the wild by identifying major causes of injury and mitigate their effects by removing the hazard where possible and by providing medical and surgical care for injured individuals so they may be again released.

It is from the latter point that I draw most of my experience having been directly involved with providing medical and surgical care to over 1200 raptors since 1972. It is the purpose of this paper to present the justification and significance of raptor rehabilitation as a management tool within the context of present day

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raptor population conditions and proposed and actual management schemes for these birds.

The reasons for managing raptors go beyond the fact that they are a wildlife resource and an important portion of the ecosystem in need of protection and conservation. Several species of North American raptors, notably the Bald Eagle, Osprey, and Peregrine Falcon have undergone precipitous declines over much of their former ranges in the last 30 years (Hickey 1969, Wetmore and Gillespie 1976). The Peregrine in particular has been completely extirpated from its range in the eastern United States and only a remnant population is left in the western United States (Fyfe et al. 1976). The documentation of the disappearance of the Peregrine at the international conference held in Madison, Wisconsin in 1965 contributed significantly to the awakening of this country to the problems of industrial and agricultural pollution and to the eventual banning of DDT in the early 1970's (Hickey 1969, Peakall 1976). Acting in concert with the pollution problem has been the widescale loss of habitat, a problem which has contributed heavily to the demise of the Bald Eagle over most of the 48 states. There are several other raptorial species such as the Merlin, Cooper's hawk, Red-shouldered Hawk, and the Marsh Hawk which are known to have undergone declines in certain locales and which, because of their particular food preferences or habitat requirements are particularly vulnerable to disturbances of these parameters. However, these 4 species lack the special dash and appeal of the Peregrine and Bald Eagle and therefore have not been given as much attention. The basic censusing data is not even available on these raptors to make a meaningful determination of their status over most of their range.

There is also a significant utilitarian reason for the management of raptors. Since the various species occupy niches at the tops of long and complex food chains and have specific requirements for nesting, they can be useful as environmental barometers. A healthy diversified, regularly reproducing raptor population in a given area implies that management programs directed toward forest and wildlife production are being conducted in accord with principles of maintaining a balanced ecosystem.

Because of the importance of raptors and the ecological information that can be obtained from monitoring and managing their populations, the USFWS in 1978 created a position within their ranks, that of a raptor biologist. Through this office there is the potential for efficiently directing and funding needed research on raptors,for standardizing census and survey techniques which will permit a synthesis of local situations into broader conclusions about populations, and to test and suggest management strategies. Through contractual and cooperative agreements there are many new opportunities for raptor research and management ahead.

Cade and others have pointed out previously that we know the necessary principles to implement management programs for raptors (Cade 1974). These principles include inventory of the breeding stock, reproductive rates, survival of various age classes, and determination of limiting factors, followed by scientific manipulation of these factors. However, because of the solitary nature of raptors, their position at the top of complex food chains, their relatively few numbers, and their great mobility the task of determining basic management parameters involves considerably more effort and expense than that required for many of the game species to which these techniques have been so successfully applied.

The censusing of nest sites and implementation of management programs for nest sites, the first of the four management approaches presented above has been very successfully accomplished in the case of the Bald Eagle population in the Great Lakes States. Broad scale censusing coverage of the eagles in these states (Minnesota, Wisconsin, Michigan, Ohio, Indiana, and Illinois) has been conducted since 1973 (Madsen 1977). Over 400 pairs of birds are observed regularly and it is estimated that over 90% of all active nest sites are included in the survey. Fixed-wing aircraft have been extensively used for making observations. The results of these surveys from 1973 through 1977 are included in Table 1. Based on the number of young produced and the relative constancy in the number of nest sites occupied, the eagle population in this area is certainly stable and shows a trend indicative of an increase.

Table 1.--Bald eagle breeding population and breeding success, Great Lakes States, 1973 through 1977. From Madsen, 1977.

	1977		1976		1975		1974		1973	
State	Occupied Nests	# Young	Occupied Nests	# Young	Occupied Nests	# Young	Occupied Nests	# Young	Occupied Nests	# Young
Wisconsin	151	181	146	139	111	112	109	103	108	107
Michigan	87	95	84	80	88	79	82	45	83	66
Minnesota	156	179	122	163	120	145	127	96	115	113
Ohio	4	1	5	2	5	3	6	2	7	2
Illinois	0	0	0	0	0	0	2	0	0	0
Indiana	0	0	0	0	0	0	0	0	0	0
Total	398	456	357	384	324	339	326	346	313	288

The Bald Eagles on the Chippewa Forest, a relatively small (6400 km^2) and intensely managed forest, have been studied since 1963 (Mathisen et al. 1977). A two-flight survey conducted in fixed-wing aircraft has been shown to provide an adequate means for detecting substantial changes in the population status of this much studied and closely monitored population (Fraser 1978). Because of the numerous studies conducted on this population of eagles, management is moving from a general approach of protecting habitat and eliminating disturbance to a specific approach involving the formulation of management plans for specific eagle territories. These specific plans take into account the tolerance of a given pair of eagles to certain types of disturbance as determined by quantitative experimentation (Stalmaster 1978), unique features of a given territory such as proximity to water, to construction work or projects involving frequent intrusion to the area for inspection or repair, and finally the potential for future alteration of the habitat by logging, dam construction, and recreational development (Mathisen et al. 1977).

By contrast other investigators studying Bald Eagles over much large tracts of land such as the 100,000 km^2 area surveyed by King (1972) or the 174,000 km^2 are surveyed by Grier (1977) chose to randomly sample their areas and make inferences about the population status and trends on that basis. Because of the differences that exist among various eagle populations with respect to habitat type and usage, and levels of human activity within eagle territories, the point has been made that for successful comparison of the results of various studies, what is needed is not complete standardization of field procedures or analytical techniques, but rather standardization of the parameters being measured (Fraser 1978).

The integration of forestry management policies with the requirements for successful and stabilized eagle production on the Chippewa National Forest are now well established. The Minnesota Department of Natural Resources with cooperation from the U.S. Fish and Wildlife Service is about to implement a management plan for eagles not nesting on public lands under federal jurisdiction. There are 44 known nesting sites of Bald Eagles outside of national forests in Minnesota (Henderson, personal communication, 1978). Land ownership status of these nest will be determined and management implemented on a recommendation basis utilizing practices that have proven to be efficacious on the Chippewa.

Specific nest site identification and protection is a useful approach for species such as the eagle where the nest is located in unique places and is frequently reused. The cliff nesting raptors such as the Peregrine Falcon and the Prairie Falcon also have readily recognized and frequently reused nest sites which would render them amenable to management programs similar to those developed for nest site protection of the eagle. For most other species of raptors, nest sites are decidedly more ephemeral and the unique common feature of sites are not as readily recognized. However, recent research on Broad-winged Hawk nest site selection (Kerans 1978) and Marsh Hawk nest site selection (Hamerstrom 1976) has shown that indeed there are some unique features sought by these birds which can be defined by continued research. Kerans (1978) concluded that in the case of the Broad-winged Hawk, the current 40 year cycle on which white-tailed deer and ruffed grouse management was based would indefinitely provide adequate nesting habitat for this species.

Of course considerations must go beyond simply the nest site and take into account the need of the parent birds for hunting, roosting, and freedom of conflict with other species of raptors. A radiotelemetry study recently completed at the Cedar Creek Natural History Area in East Central Minnesota (Fuller 1979) provides data on the spatial and temporal partitioning of woodland habitat by resident raptors, providing forest managers with yet another set of parameters to place in their management equation.

Another approach toward eagle management in the Upper Mississippi region is that of protecting wintering roost sites. A private organization, the Eagle Valley Environmentalists, has been the main promoter and executor of this concept since 1972. Their approach has been to identify sites where large numbers of eagles roost at night and raise money to buy the land on which these sites are located, or enter into easement agreements with landowners to insure preservation of the roost site on a long term basis. Without downplaying the importance of wintering habitat for eagles, other investigators have advised caution in the large scale outlay of public and private money to buy eagle roost sites outright since the occupancy of these sites is affected by local annual variations in weather and food availability (Grier 1977).

The second approach to raptor management for which there are some programs currently implemented is that of insuring uncontaminated food supplies. Whereas toxicity to raptors due to the food chain transfer of agricultural pesticides and industrial pollutants has been well established as in the case of the Peregrine Falcon, the hazard of secondary toxicity from lead pellets ingested with the flesh of prey species has only recently been recognized (Locke 1969, Mulhern et al. 1970). Locke (personal communication 1978) has autopsied 15 Bald Eagles in which secondary lead poisoning was suspected and later confirmed in nine of them. This author has seen secondary lead poisoning in 3 Prairie Falcons, 1 Goshawk, and 1 Bald Eagle. Among raptors the Bald Eagle is particularly vulnerable to secondary lead poisoning since they frequently scavenge on crippled ducks and geese during and after the waterfowl season. It is believed that toxicity occurs because of a failure of the pellet casting mechanism to cause expulsion of the pellets. Studies are currently underway at the University of Wisconsin (Temple and Friend) and at the University of Minnesota (Hennes, Frenzel, Duke, Redig, and Henderson) to assess the magnitude of secondary lead poisoning in eagles. It is likely that management decisions affecting the use of lead shot in certain waterfowl hunting areas will be forth coming based on this research.

The continued pesticide contamination of arctic Peregrine Falcons is an example of a food contamination problem for which the implementation of remedial management is not immediately possible. These birds are highly migratory and many pass along the Gulf Coast of Texas each year enroute to wintering areas in Central and South America (Rogers & Hunt 1975). It appears that the very heavy utilization of DDT in these countries is the source of contamination for these birds and their migratory food supplies (Burnham 1978). It has been suggested by resolution at the Raptor Research Foundation in 1976 that chemical pesticides deemed unsuitable for use in the United States not be allowed export abroad by American manufacturers.

Another management scheme that has been proposed for these arctic Peregrines to protect them from heavily contaminated prey is shortstopping (Cade 1974). Migrant Peregrines on southward passage would be trapped, held over the winter by qualified individuals, and released in following springs at 1,2, or 3 years of age to migrate back to the tundra free of pesticide loads. To date this idea has not been implemented.

The third approach to raptor management, that of augmenting production, has taken several forms. The various methods have included transferring healthy eggs or young birds from successful nests to active sites with a history of repeated failure (Madsen 1977,Burnham 1978), encouraging multiple clutching to occur by removal and artificial incubation of the first set of eggs (Cade 1974, Burnham 1978), captive production of birds and subsequent release into the wild by fostering them into remaining active wild nests or by controlled reintroduction where no wild birds exist (Fyfe 1976, Sherrod and Cade 1978). Increasing the number of available nest sites has been done for Ospreys (Ames & Mersereau 1964, Postupalsky 1974) for Prairie Falcons (Olendorff & Stoddard 1974), for Red-tailed hawks and Great-horned Owls (Grewe 1976), and for Kestrels (Hammerstrom 1974). The specifics of two cases of augmentation are illustrative.

Several Bald Eagle nests along the east coast of Maine had a history of reproductive failure spanning 10-12 years due to heavy pollutant contamination of the adults. A scheme requiring the transfer of healthy partially incubated eggs from Minnesota and Wisconsin nests was proposed. The first Bald Eagle egg transplant was conducted in 1974. Three eggs, comprising two complete clutches, were taken from two nests in Minnesota after 21 to 26 days of incubation. One egg was accidentally destroyed during placement in an active nest. The remaining two eggs were placed in separate unproductive nests in Maine. One addled egg found in each of the two Maine nests was removed at the time of the transplant. Both Minnesota eggs hatched under the foster parents. One eaglet disappeared after 10 days and one successfully fledged. Single dummy eggs were placed in the two Minnesota nests at the time their eggs were taken to hold the birds on their territories. One pair incubated the dummy eggs 10 days before deserting, while the other pair immediately abandoned the nest site. These nests were not reoccupied in 1974, nor were the same nest sites used in 1975 and 1976. It is not known if the donor pairs used alternate sites. In Maine, neither of the 1974 recipient nests was reused in 1975; one was reused in 1976. An alternate nest was used by one pair in 1975 but the other pair is not believed to have utilized an alternate nest. In sum, in 1974 three eggs were removed from two nests in Minnesota and one eaglet was successfully fledged in Maine.

In 1975, the second Bald Eagle egg transplant was conducted. Four eggs were taken from two nests in Wisconsin. One egg was placed into each of four nests in Maine. One egg was not accepted by the foster parents. Of the three eggs incubated, two hatched and one eaglet fledged. Five of six eggs and shell fragments of a seventh egg found in the four Maine nests were removed at the time of transplant. There were 39 active nests located in Maine in 1976 and six to ten were candidates for transplanted eggs. Although still active, the candidate nests had at least a five year history of failure. These nests were located along the Atlantic Coast, Penobscot River drainage, and Moosehead Lake. Eight Bald Eagle eggs were transplanted from two nests in Wisconsin and two nests in Minnesota. Of the eight eggs taken from the lake states, two eaglets fledged (Madsen 1976).

The Peregrine Falcon has been the subject of a large scale breeding and release program conducted in the United States by the Peregrine Fund at Cornell University (Sherrod and Cade 1978) and by the Canadian Wildlife Service in Alberta, Canada (Fyfe 1976). At Cornell from 1970 through 1977, 229 falcons have been produced of which 133 were released by various methods between 1974 and 1977. In 1976 and 1977 a few of these released birds were observed returning to their release sites and there is one known instance where a captively reared female has paired with a wild male and produced offspring (Cade 1977). Grier (1976) estimated that, based on regular rates of production and mortality for healthy peregrine populations, the release of 250 falcons per year for 15 years would be required to re-establish the Peregrine east of the Mississippi River to approximation of its former level. The results of the captive rearing program have so far been very encouraging, but it will be a few more years before any reliable forecasts of the eventual outcome can be made.

The last of the four management approaches to be discussed is that of reducing mortality. The primary thrust in this regard has been the grass roots development of a large number of so-called raptor rehabilitation programs across the country over the last eight to ten years. A survey was conducted during the summer of 1978 to document the magnitude of raptor rehabilitation in the United States (Duke, Clarke, and Redig). 500 questionnaires were mailed out to individuals who had now or at one time held a federal permit for tending to injured raptors or had otherwise expressed an active interest in the subject; 202 replies were received. A 3 years total of 5,329 raptors of 39 species was reported. Since there are a sizeable number of raptors being submitted to these programs, examination of the reasons for admission of injured birds could reveal some of the signficant causes of injury and mortality among raptors. This type of information as well as success rates were sought by the original questionnaire; however, due to many inconsistances in record keeping among respondents, the information is not presently too significant. A standardized record keeping and summary form is now being drafted for use by all persons holding rehabilitation permits and will be distributed through the Raptor Information Center.

The records from our own program do provide an insight into the numbers and types of injuries incurred by raptors in this region and the type of success that can be realized from a rehabilitation effort. Table 2 is a list and a tally of the raptors we have handled at the University of Minnesota from April 1, 1972 through December 31, 1978. Table 3 is a summary of the problem categories for which these birds listed in Table 2 were submitted. Table 4 is a specific breakdown of problem categories for Eagles and Peregrine Falcons for 1977.

Approximately 75% of the raptors handled were presented for traumatic injuries; in most instances there were fractures of one or more of the long bones. In recent years techniques have been described for the anesthesia of raptors (Redig and Duke 1976, Paddleford 1978) and for the reduction and fixation of fractures of the long bones of raptors (Redig and Rausch 1978). The degree of success achieved in the repair of fractures and other injuries has depended upon which bone was broken, the duration of time since the injury, the severity, and the cause. Prognostic evaluations can be made only by a clinician with experience in handling avian fractures. Rehabilitation goes far beyond caring for the obvious fracture or injury, requiring expenditure of time, effort, and expertise in providing adequate housing, nutrition, and vigilance against the development of other diseases and problems to which raptors are susceptible.

The category that has proven to be the most difficult to handle is trap-induced injuries. In any given year these injuries comprise about 16-20% of our admissions and have the lowest chance for successful repair. Table 5 is a cumulative listing through 1977 of all raptors admitted with trap injuries. Table 6 is a specific listing of trapped eagles. Only 3 out of 15 trapped eagles were released and these were all partial amputees. Most of the trapping incidents involved eagles caught in open-baited traps set for furbearing animals during the winter. Trapped limbs freeze quickly and there is no chance for rejuvenation of frozen tissue. However, we have several instances on record where the limb did not freeze but the impact of the trap caused sufficient soft tissue damage to lead to vascular destruction and subsequent loss of the limb below the injury site some 10-14 days after the injury. Because of these types of findings, I take exception to the investigators who recently reported raptors caught in traps in the conduct of turkey predation study could be released if damage was confined only to bleeding at the trap injury site or only one broken leg (Beasom 1974).
Another sequelae observed in birds with trap or frostbite injuries is the development of vegetative and septic endocarditis, that is bacterial colonization of the heart valves following the introduction of organisms at the wound site with embolic transfer via the blood stream to the heart and occasionally the brain, (Wallach and Fleig 1969, Angrist _et al_. 1960, Redig 1978). The subsequent potential for cardiac malfunction is sure to shorten the life span of the animal. It would seem that this trapping problem could be managed by restricting the use of open bait sets and by educating the trapping public to the hazards their activities may have for non-target wildlife.

Table 2.--Species and numbers of raptors admitted for treatment at the University of Minnesota from April, 1972 through December 31, 1978.

Red-tailed Hawk	238	Goshawk	40	Screech Owl	58
Red-shouldered Hawk	15	Merlin	2	Burrowing Owl	1
Broadwinged Hawk	101	Kestrel	149	Saw Whet Owl	18
Swainson's Hawk	6	Prairie Falcon	29	Boreal Owl	1
Ferruginous Hawk	6	Peregrine Falcon	15	Barred Owl	58
Rough-legged Hawk	52	Gyrfalcon	5	Great-Gray Owl	3
Harris' Hawk	1	Bald Eagle	101	Long-eared Owl	27
Marsh Hawk	13	Golden Eagle	20	Short-eared Owl	20
Sharp-Shinned Hawk	20	Osprey	16	Snowy Owl	24
Cooper's Hawk	16	Turkey Vulture	5	Great Horned Owl	215
				TOTAL	1,275

Table 3. Summary of causes of injuries to raptors submitted to the University of Minnesota.

Injury	1972-1974	1975	1976	1977	1978	Overall
Projectile	34	35	23	16	13	24
Traps	25	12	8	7	4	11
Accident	22	30	37	46	49	37
Disease	8	5	12	8	2	7
Orphaned	3	10	15	12	14	11
Other	8	8	5	10	18	10

Table 4. Breakdown of problem types for which Eagles & Peregrine Falcons were submitted in 1977.

	Eagles		
	Bald	Golden	Peregrines
Projectile	6	5	1
Trap	3	1	
Accident	7	1	2
Starvation	2		
Orphan	5		
Other	3		

Table 5. Listing of all raptors submitted for treatment of trap-induced injuries, other than pole traps.

Species	Year/Number				
	1974*	1975	1976	1977	Total
Great Horned Owl	5	5	9	5	24
Snowy	1			1	2
Barred Owl		2			2
Screech Owl	1				1
Red-tail		9		3	12
Rough-legs	1	1	1	3	6
Marsh Hawk			1		1
Broadwing				1	1
Kestrels		1			1
Bald Eagles	2	1	1	6	10
Golden Eagles	1		1		
Totals	11	19	13	19	62

*Records prior to 1974 are inaccurate except for eagles.

Table 6. Listing of Bald and Golden Eagles submitted for treatment of trap-induced injuries. From Redig (1978).

	Clinic #	Locale of Origin	Fate
1973	1	Paynesville, MN	Released after amputation of DII
	2	Hastings, MN	Released after amputation of DIII
	3	Brainerd, MN	Died
1974	A-4	Benson, MN	DOA
	A-75	Detroit Lakes, MN	Died after surgery to repair fracture
(Golden)	A-105	Fergus Falls, MN	Died
1975	B-129	Michigan	Held as a 1-footed cripple
1976	C-193	Fergus Falls, MN	Died after foot was lost
(Golden)	C-203	Illinois	Died
1977	D-29	Rhinelander, WI	Foot amputated-bird died later
	D-206	Michigan	Foot amputated locally-DOA
	D-271	S. Dakota	Both feet destroyed-bird died
	D-274	Fergus Falls, MN	Released with slight damage to DIII
	D-298	Ely, MN	Halux destroyed-bird crippled
	D-306	Alexandria, MN	Both feet destroyed-bird died

Total # of trapped eagles died - 10
Total # of trapped eagles crippled - 2
Total # of trapped eagles released - 3

Another subtle problem whose actual statistics are buried in the "accident" category is that of raptor collisions with power lines. Nelson (1978) and Crawford et al, (1974) have documented the electrocution of raptors by power lines and suggested management remedies. The injuries referred to here are not electrocutions, but simple collisions resulting in fracture of the wings usually. Fitzner (1975) briefly described this hazard for owls. In 1978 alone our program has received 2 Bald Ealges, 2 Ospreys, 1 Golden Eagle, 1 Broad-winged Hawk and 1 Peregrine Falcon which were injured by flying into wires. In all cases the injured birds were found adjacent to high tension power lines and no other cause of injury was found upon examination. One Osprey was admitted with a fractured coracoid; all others received fractures to the wing bones proper. The significance of this type of injury in light of the many other means by which much larger numbers of birds are destroyed may be questioned, nevertheless, the birds do hit wires and there are more and more high tension lines being strung completely across Minnesota and elsewhere. It is conceivable that these lines could have some significant effects on local populations of raptors.

One of the measures of success of such a program is the disposition of the birds treated. Table 7 is a summary of our attempts through 1977 and Table 8 is a specific summary of the disposition of Eagles and Peregrine Falcons (Redig 1978). Of even more significance is the survivability of rehabilitated raptors after they are released. Approximately 500 raptors have been released from this program with all birds bearing conventional USFWS bands. So far returns have been reported on 5 of these birds with survival rates ranging from 2 weeks to 4 months. More useful information has been obtained from a color marking scheme employed for Bald and Golden Eagles in addition to banding. Of 28 eagles marked with vinyl wing markers, subsequent sitings have been made on 8 birds. Two of these birds were released on the Swan Lake Refuge in Missouri in 1976 (Griffin and Redig) and their progress followed through February when the mass of wintering eagles departed the refuge. Another young eagle released at the Montezuma Wildlife Refuge in Upstate New York in early September was followed for 6 weeks before it became entangled in barbed wire and died. Postmortem examination of this bird revealed that it was in a good nutritional state. Another adult eagle marked and released on 3/19/76 was reported during the spring of 1978 to be occupying a nest with young eagles near Harris, Minnesota. And another adult released on 12/28/73 was found in June, 1974 by Chuck Sindelar at a Wisconsin nest with 2 young in the nest. One last example is an eagle originally shot near Oshkosh, Wisconsin on 6/8/76, banded and released on 9/4/76 at Duluth, and seen

Table 7. Summary of rehabilitation attempts for all species of raptors (Percentages in each year). From Redig (1978).

	1975	1976	1977	Overall
Died	30	22	15	22
Destroyed	3	8	11	7
Holding	8	13	9	10
Research	16	15	10	14
Successfully Rehabilitated	43	43	39	42
Pending*	0	0	16	5

* Indicates raptors not ready for release at end of the year, but for whom complete recovery is anticipated.

Table 8. Disposition of eagles and peregrines (Percentages in each year). From Redig (1978).

	1972-1974	1975	1976	1977	Overall
Died	47	27	41	18	33
Holding	0	7	0	11	3
Research	26	13	18	19	19
Successfully Rehabilitated	27	53	31	26	37
Pending	0	0	0	26	8

again on 9/5/76 3 miles north of the release site and again in mid-January on the Swan Lake Refuge in Missouri.

During the spring of 1978, 5 nestling Bald Eagles were brought in at various times after they had been blown from their nests during storms. 3 of these birds were admitted with leg fractures. Approximate age of the birds at the time of admission ranged from 3 weeks to 12 weeks. The two uninjured birds were given physical examinations, held for a week of observation, and then fostered back to other 1 chick eagle nests. One of these birds was approximately 4 weeks old and the other 12-13 (nearly fledged) at the time fostering was done. No serious aggression with other eagle chicks or problems with adult acceptance were observed during subsequent observations. Of the other 3 chicks, one had fractures in both legs and convalescence was not complete until mid-September. He was not released, but rather placed in a captive breeding project. Both of the other birds underwent surgical repair of their tibio-tarsal fractures and completed convalescence before the end of the eagle nesting season. One bird was put back in a nest near Drummond, Wisconsin on July 1, 1978. There was a single chick in the nest about 2 weeks younger than the rehabilitated bird. There was momentary aggression between the two chicks manifested by threat postures, but no contact. Ground checks made on July 3,4, & 5th revealed only one bird in the nest; on July 6th, 2 chicks were seen sitting on the edge of the nest.

The remaining rehabilitated bird was taken to a nest near Minong, Wisconsin on July 15, 1978. Again there was 1 chick, nearly ready to fledge in the nest. The new bird was placed in a dead snag 30 m from the nest tree and about 5 m off the ground. No observations were made until July 20th at which time 1 chick of uncertain identity was seen in the nest and 1 adult in the nest tree. On July 28th the color marked youngster was observed in a tree about 200 yards from the nest tree. The unmarked youngster was not seen at that time.

Color marking of rehabilitated eagles clearly yields much more information concerning the post-release survival of these birds. The limited data available so far indicates that in fact these birds will survive and even resume apparently normal patterns of migration and reproduction. Because the post release survivability of rehabilitated birds is important information to have, the time is right for a program of radio tracking of these birds following release to learn more about their reintroduction into the wild.

Clearly, rehabilitation of raptors provides two avenues of direct benefit to the resource, 1) the accumulation of data regarding the causes of raptor injury and mortality on both a regional and national level, and 2) the return of a significant number of individual birds, particularly eagles, to the wild.

By expanding the scale of these operations there is the potential for the recovery of many more raptors. The magnitude of the beneficial effects can be enhanced by promoting centralization of efforts so that there is increased continuity in the learning from old mistakes and application of new techniques and by increasing the level of funds available for this work.

There are also signficant indirect effects that are realized from the project underway at the University of Minnesota. By conducting this work at a veterinary college within a major university, the opportunity is presented to teach concepts and techniques of avian research and medicine to veterinarians and wildlife students who in turn can relate this information to many other people throughout their careers. Crippled birds, unsuited for release are available for use by students and researchers to conduct controlled laboratory testing of hypotheses that can lend significant insight into field observations. Utilization of injured raptors for research in behavior, medicine, surgery, pathology, toxicology and other fields, is possibly the single most important aspect of any rehabilitation project. Such research is a source of new information that will be used in the years to come to provide improved methods for the management of raptors in the laboratory and in the field (Redig 1978).

Lastly, there is a significant benefit to be realized by utilizing material depicting the plight of injured raptors to sensitize the members of the public to the need for raptor and wildlife conservation. Photographs, X-rays, and crippled live specimens can create lasting impressions on the minds of people who wouldn't otherwise be concerned about injured raptors. By increasing the levels of awareness and appreciation for raptors and wildlife among the public, it is hoped that not only the direct mortality-causing effects of human activity, such as shooting and trapping, may be reduced, but also the indirect effects of habitat destruction may be realized and mitigated.

If the whole matter of raptor management appears thin and shallow at this point the reason is likely to be related to the recency of its application. Prior to the mid 1960's, most raptor management was directed toward their destruction; research primarily documented declines in populations for select species. The first significant attempts at management were seen directed toward the Bald Eagle in the mid-to-late 60's, followed by augmentation efforts to save the Peregrine in the early 70's, which efforts have yet to prove their management potential. Reducing mortality by removing hazards and repairing injured raptors is similarly only recently being developed and has yet to be proven a significant tool in the overall scheme. Certainly this multifaceted approach provides a much brighter future for the raptors than was thought possible 10 years ago, but the work is just barely started.

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COMPILATION OF AVIAN INFORMATION IN COMPUTERIZED DATA STORAGE AND RETRIEVAL SYSTEMS OF THE NORTH-CENTRAL AND NORTHEASTERN UNITED STATES

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Abstract.--Characteristics of 18 computerized files of bird information in the North Central and Northeast United States were compiled. Information contained in the files included species occurrence, population and management requirements. No standard framework for data files was identified from the 18 custom built systems. Expected expansion and development of new systems necessitates improved communication to establish standard definitions for identifying, describing and coding data elements.

INTRODUCTION

Many computerized data/information systems are currently in use or being developed to store and retrieve information about nongame species of birds. We were asked to review and summarize systems with data from the North Central and Northeastern part of the United States. Our review is cursory. To provide a brief overview on this subject, we called system managers and others, asking a series of questions about their system. In this report we have categorized information available by species occurrence, populations, and management requirements. We suggest individuals identified in the Appendix be contacted directly for detailed information about systems. We apologize for those systems we inadvertently overlooked. The assistance of Mr. Ralph Alig in preparation of this report is deeply appreciated.

CHARACTERIZATION OF DATA STORAGE AND RETRIEVAL SYSTEMS

We identified 18 computerized files which contain some information about birds in the N.E./N.C. part of the United States (Table 1). Approximately one-third of the files contain a list of all categories of birds (Table 1). Species lists for waterfowl, shorebirds, u land gamebirds, raptors and migratory birc are available from approximately two-thirc the files. Passerine, non-migratory, and bird species lists were included in nearly half of the files.

Fifteen files have data at the state level. Less than half of the files have species lists at the regional level. Spec lists for political units smaller than the state are available from about one-third c the files. A continental United States li was found in eight files.

Fourteen files contain information ab categories of birds associated with variou vegetation types. Twelve files produce a by ecosystem (combinations of vegetation types). Five of the files will provide a species list by the following ecological categories: biome, ecosystem, vegetation stage of succession, community structure a specialized habitat such as cavities, snag riparian, etc.

Population Estimates

Fourteen files have population estima or population trends for some category of birds (Table 2). Population estimates are available in nine information bases. Wate fowl are the most common category of birds which we have population estimates. No po lation information is computerized for pas ine bird populations except for species th

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threatened or endangered. The State is most common unit of political organization population data. Continent-wide population imates are not available. The biome and system level of ecological organization for ulation estimates are represented in the t information bases.

Population trends for gamebirds are best resented; however, two information bases tain trend information for passerine birds. cialized habitats are the lowest ecological el represented and are present in four of information bases.

Compared to species occurrence infor-ion, population estimates or trends are h difficult and expensive kinds of infor-ion to obtain for data systems. The ber of systems containing these types of ormation reflect this fact.

Management Requirements

Six files have some population manage-t information defined by protection or vest quotas (Table 3).

Habitat requirements of bird species can effectively used in developing habitat agement programs and are the most common agement type of information available from puterized data storage and retrieval stems (Table 3). Ten of the information es contain species habitat requirements. pared to other kinds of information for -game birds, they are well represented in ta systems by information on habitat require-nts. Habitat management guidelines are most ailable for game species; however, manage-t guidelines for non-game bird habitat cur in four files.

How Much of What They Require is Available?"

Effective evaluation of alternative nagement practices and mitigation require measure of habitat tradeoffs. Quantities available habitat in units of land area e a useful measure in analyzing the conse-ences of changing habitats. Seven files ntain estimates of habitat quantities. veral other wildlife files have defined ecies habitat requirements which permit a nk to data files which contain estimates of bitat quantities.

SUMMARY

Computerized files containing information out birds in the Northeastern and North ntral United States are varied. The 18 les reviewed were custom built and programmed; there is no standard framework. The 1979 RPA Wildlife and Fish Assessment data base is the only file which contains information on the habitat requirements of all categories of birds in all states, territories and possessions of the United States.

Increased use of automated systems for storing and retrieving information on sensitive or threatened and endangered species is noticeable. Many data base managers contacted in this study indicated they were hoping to expand their data files or develop new ones. Several individuals interviewed said population estimates or trends will be increasingly computerized. Desired population sizes are another area of noticeable potential expansion and improvement.

Management guidelines seem to be drawn mostly from literature searches and are not frequently stored or accessed in the computer. Habitat requirements are also largely drawn from the literature, but more easily lend themselves to computerized storage and retrieval systems. The reason for the difference is the more general applicability of habitat requirement information and various ecological situations compared to management guideline information.

The emphasis of avian information in automated systems has been placed on game or threatened and endangered species, with non-game categories being less developed. There is a lack of communication between system developers and/or users with similar personnel in other regions or states.

A major recommendation is to form a data standards group for the region and attempt to use standard definitions in collecting information about birds.

Table 1.---Availability (X) of Bird Species lists in the Northeastern and North Central United States from Computerized data storage and retrieval systems

Type of Information	System Acronym or Identification Key																	
	USDI/BBS	USDI/BBC	USDI/CMBD	USDI/RUN WILD EAST	USDI/MBMO	CORNELL/ IFIF	CORNELL/ Nest	DOD/SWIS1/	U. of MN.	USDI/M. Dove	USDI/W - Cock	U. of Maine	ME/MIDAS	CAR. MUS./ Band	NY/B.W.	NAT. CONS./ LCDSF	USDA/WAFA	MD/MAGI
Category of Birds																		
Waterfowl	X	X	X	X	X		X	X					X	X		X	X	X
Shorebirds	X	X	X	X		X	X	X						X		X	X	X
Upland Gamebirds				X			X	X	X	X	X		X	X	X	X	X	X
Passerine	X	X		X			X	X						X		X	X	X
Migratory	X	X	X	X	X	X	X	X					X	X		X	X	X
Nonmigratory	X	X		X		X	X	X						X		X	X	X
Raptors	X			X			X	X	X			X	X	X		X	X	X
Seabirds			X				X	X				X	X	X		X	X	X
Political Units																		
Continental U.S.	X	X	X			X	X							X		X	X	
Region	X	X	X		X	X	X									X	X	
State	X	X	X	X	X	X	X	X		X	X		X	X		X	X	X
County				X		X		X					X	X		X		X
Township						X						X	X	X		X		X
Other 2/									X	X		X	X		X	X		X
Ecological Units																		
Biome	X	X	X		X	X		X					X			X		X
Ecosystem	X	X	X		X	X	X	X				X	X			X	X	X
Vegetation Type	X	X	X	X	X	X	X	X	X	X			X			X	X	X
Seral Stage						X	X	X					X			X	X	X
Community Structure		X	X			X	X	X					X			X		X
Specialized Habitats		X	X	X		X	X	X				X	X			X	X	X

1/ System includes information about birds classified by the F&WS as threatened or endangered of extinction.

2/ Includes a research area, physiographic regions, wildlife management units, F&WS-numbered islands, New York's thousand square kilometer inventory blocks, USGS geological quads, and Maryland's state inventory blocks (≃100 acres each)

Table 2.---Availability of estimates (E) and trends (T) in bird populations in northeastern and northcentral United States from computerized data storage and retrieval systems

Type of Information	System Acronym or Identification Key																	
	USDI/BBS	USDI/BBC	USDI/CMBD	USDI/RUN WILD EAST	USDI/MBMO	CORNELL/ IFIF	CORNELL/ Nest	DOD/SWIS	U. of Minn.	USDI/M. Dove	USDI/W - Cock	U. of Maine	ME/MIDAS	CAR. MUS./ Band	NY/B.W.	NAT. CONS. LCDSF	USDA/WAFA	MD/MAGI
Category of Birds																		
Waterfowl	T		E	T	E			E					E				E,T	E
Shorebirds	T		E	T		E		E										E
Upland Gamebirds				T				E	E	T	T		E		T		E,T	E
Passerine	T			T	E			E										E
Migratory	T					E		E					E					E
Nonmigratory	T					E		E										E
Raptors								E	E			E	E					E
Seabirds			E					E				E						E
Political Units																		
Continental U.S.	T																	
Region	T		E		E	E												
State	T		E	T	E	E					T	E	E				E,T	E
County			E			E							E					E
Township			E			E						E	E					E
Other 1/									E	T		E	E		E			E
Ecological Units																		
Biome	T		E		E			E					E					E
Ecosystem	T		E		E							E	E					E
Vegetation Type	T		E		E					T			E					E
Seral Stage			E										E					E
Community Structure			E										E					E
Specialized Habitats			E									E	E					E
Non-ecological Units																		

1/Includes a research area, wildlife management units, physiographic region, F&WS-numbered islands, and New York and Maryland inventory blocks.

Table 3.---Availability of Management information for Bird species in Northeastern and Northcentral United States from computerized data storage and retrieval systems

Management Information Category of Birds	System Acronym or Identification Key																	
	USDI/BBS	USDI/BBC	USDI/CMBD	USDI/RUN WILD EAST	USDI/MBMO	CORNELL/ IFIF	CORNELL/ Nest	DOD/SWIS	U. of Minn.	USDI/M. Dove	USDI/W - Cock	U. of Maine	ME/MIDAS	CAR. MUS./ Band	NY/B.W.	NAT. CONS./ LCDSF	USDA/WAFA	MD/MAGI
Desired Population Size (H, P)[1]																		
Waterfowl				H	H			P					P					
Shorebirds				H				P										
Upland Gamebirds				H				P					P		H			
Passerine				P	E			P										
Migratory								P					P					
Nonmigratory								P										
Raptors				P				P				P	P					
Seabirds			E					P				P	P					
Habitat Requirements (F, B, S)[2]																		
Waterfowl		B,S	F,B,S	F,B				F,B,S					F,B,S			F,B,S	F,B,S	F,B,S
Shorebirds		B,S	F,B,S	F,B		B,S		F,B,S								F,B,S	F,B,S	F,B,S
Upland Gamebirds				F,B				F,B,S					F,B,S			F,B,S	F,B,S	F,B,S
Passerine		B,S		F,B				F,B,S								F,B,S	F,B,S	F,B,S
Migratory		B,S	F,B,S			B,S		F,B,S					F,B,S			F,B,S	F,B,S	F,B,S
Nonmigratory		B,S				B,S		F,B,S								F,B,S	F,B,S	F,B,S
Raptors				F,B				F,B,S				F,B,S	F,B,S			F,B,S	F,B,S	F,B,S
Seabirds								F,B,S				B,S	F,B,S			F,B,S	F,B,S	F,B,S
Habitat Management Guidelines (F, B, S)[2]																		
Waterfowl		B,S	F,B,S	F,B				F,B,S										
Shorebirds		B,S,	F,B,S	F,B				F,B,S										
Upland Gamebirds				F,B				F,B,S										
Passerine		B,S		F,B				F,B,S										
Migratory		B,S,	F,B,S					F,B,S										
Nonmigratory		B,S						F,B,S										
Raptors				F,B				F,B,S				B						
Seabirds								F,B,S				[illegible]						

[1] H = Harvest Regulation, P = Protection Regulation.

[2] F = Feeding, B = Breeding, S = Seasonal.

S tem Ac nym or ey	Name of Contact Individual and Address	System Is Available for Transport to Other Computer Centers	Computer Language	Type of Computer and Model	Data Can Be Obtained Through	Fee for data on the system, if any	Input Mode	Output Mode	Location of Computer Facility
UI/ E	Danny Bystrak Migratory Bird and Habitat Lab Patuxent Research Center USDI Fish and Wildlife Service Laurel, MD 20810	no	FORTRAN	IBM 370-150	Bystrak	none for reasonable requests	cards, tape, disc	printer	Patuxent Research Center USDI Fish and Wildlife Service Laurel, Maryland
UI/ E	Chandler Robbins Patuxent Research Center USDI Fish and Wildlife Service Laurel, MD 20810	no	FORTRAN	IBM 370-150	Robbins	none for reasonable requests	tape, disc	printer	Patuxent Research Center USDI Fish and Wildlife Service Laurel, Maryland
UI C	Stanley Anderson Patuxent Research Center USDI Fish and Wildlife Service Laurel, MD 20810	yes	FORTRAN	IBM 360-60	Anderson	none for reasonable requests	inter-active	inter-active	Interior Bldg. Washington, D.C.
UI/ RUWILD ET	Douglas Gladwin Eastern Energy & Land Use Group Harpers Ferry Center Harpers Ferry, WV 25425	yes	FORTRAN	Univac 1108	Edgar Pash EELUG Harpers Ferry Ctr Harpers Ferry, WV	tape cost ($12.00)	cards	inter-active	Arizona State University Tempe, Arizona
UI/ M	Richard Pospahala Migratory Bird Management Office USDI Fish and Wildlife Service Laurel, MD 20810	yes	COBOL	IBM 370-115	Pospahala	none, for reasonable requests	cards, tape	printer	Patuxent Research Center USDI Fish and Wildlife Service Laurel, Maryland
Coell/ IF	Donald McCrimmon Laboratory of Ornithology Cornell University Ithaca, NY 14850	yes	FORTRAN	IBM 370-168	McCrimmon or the Cornell Univ. Comp. Ctr.	yes, fee schedule depends on volume used	cards, tape	cards, tape printer	Cornell Univ. Ithaca, New York
Coell/ Nt	Donald McCrimmon Laboratory of Orinthology Cornell University Ithaca, NY 14850	yes	FORTRAN	IBM 370-168	McCrimmon or Cornell Univ. Comp. Ctr.	Same as above	cards	cards, tape printer	Cornell Univ. Ithaca, New York
D/ SS	Tony Rekas Corps of Engineers Vicksburg, MS 39180	possibly	FORTRAN	GE 635	Rekas	none	inter-active	printer inter-active	Corps of Engineers Vicksburg, Mississippi
NY B.	William Sarbello Biometrics Unit Wildlife Resources Center Bureau of Wildlife DN. of Fish and Wildlife Delmar, NY 12054	no	FORTRAN and COBOL	Honeywell 60-60	Sarbello	none at present	cards tape disc inter-active	cards tape printer	Empire State Plaza Albany, New York
Na Co./ LCF	Helmut Moyseenko The Nature Conservancy Suite 800 1800 N. Kent Street Arlington, VA 22209	yes	FORTRAN	IBM 360-65	Moyseenko	yes, at cost	cards tape disc	printer inter-active	American Management Systems Lynn Street Arlington, Virginia
US/ WA	Thomas Hoekstra Research Wildlife Biologist RM Forest and Range Exp. Stn. USDA Forest Service 3825 E. Mulberry Fort Collins, CO 80526	yes	FORTRAN	Univac 1100-42	Hoekstra, Forest Service regional staff biologists, or Dennis Schweitzer, USDA FS, WO	none, for reasonable requests	cards	cards tape printer	USDA Fort Collins, Colorado 80524
MD MA	John Antenucci State Planning Office-Maryland Baltimore, MD 21200	yes, but only under special arrangements	FORTRAN	Univac 1108	Antenucci	yes, at cost	cards tape disc remote-batch inter-active	printer	Univ. of Maryland College Park, Maryland

System Acronym or Key	Name of Contact Individual and address	System Is Available for Transport to Other Computer Centers	Computer Language	Type of Computer and Model	Data Can Be Obtained Through	Fee for data on the system, if any	Input Mode	Output Mode	Location of Computer Facility
U. of Minn.	John Tester Dept. of Ecology and Behavioral Sciences or Kathleen Cinnel 317 Zoology Bldg. Univ. of Minnesota St. Paul, MN 55108	yes	FORTRAN	Central Data Corporation Cyberg 74	Cinnel	yes, reimbursment for computer time and personnel costs involved	cards	printer	Univ. of Minnesota St. Paul, Minnesota
USDI/ M. Dove	David Dolten or Robert Shanahan Patuxent Research Center USDI Fish and Wildlife Service Laurel, MD 20810	yes	FORTRAN	IBM 370-115	Dolten	yes, but not specified	tape	printer	Patuxent Research Center Gabrielson Lab. Laurel, Maryland
USDI W-Cock	John Totten Patuxent Research Center USDI Fish and Wildlife Service Laurel, MD 20810	no	COBOL	IBM 370-65	Totten	none	tape	printer	Patuxent Research Center Gabrielson Lab. Laurel, Maryland
U. of Maine	Bucky Owen or Stewart Fer Cooperative Wildlife Research Unit Univ. of Maine Orono, ME 04473	yes	FORTRAN	IBM 360	Owen	none	cards, tape	cards tape disc printer interactive	University of Maine Orono, Maine
ME/ MIDAS	Arthur Ritter or Frederick Hurley Dept. of Inland Fisheries and Wildlife, Statehouse Off. Bldg. Augusta, ME 04330	yes	FORTRAN	Honeywell 6000	Ritter	yes, cost plus 60%	cards, tape	printer	Statehouse Office Bldg. Augusta, Maine
CAR. MUS./ Band	Mary Clench, Assoc. Curator of Birds or John Sutton, Data Services Carnegie Museum Pittsburgh, PA 15200	yes, but only under special arrangements	FORTRAN	IBM 370	Sutton or Clench	yes, at cost	cards, tape	printer	MACH 4 (Commercial Services System) Cleveland, Ohio

NONGAME BIRD HABITAT MANAGEMENT IN NEW JERSEY FORESTS

Joan M. Galli[1]

Abstract -- A brief review is presented of research and management programs for nongame forest-dwelling birds in New Jersey. Particular emphasis is given to the state wildlife management agency's programs.

INTRODUCTION

Today, our attention is directed speifically at agency sponsored programs to anage forest habitat for nongame birds. Let e begin by providing a brief summary of New ersey's forest and wildlife resources that ill place our management programs in perective.

The 2.1 million acres of forest in New ersey are concentrated in two areas. The ine Barrens, encompassing approximately one illion acres, is located in the southern uter Coastal Plain portion of the state. his woodland has been described as the "most xtensive wildland tract of the Middle tlantic Seaboard region" (McCormick 1971). ominant species are pitch pine (*Pinus regida*), aks (*Quercus spp.*) and southern white cedar *hamaecyparis thyoides*). The second conentration of forest lands, dominated by mixed ak, occurs on the ridges of the Northern Highands and in the Ridge and Valley province in orthwestern New Jersey. In the remaining eas of the state, urban sprawl and agricultural practices have reduced forest lands to cattered woodlots of various sizes along idges and poorly drained lowlands.

Since 1899, the proportion of forest and in New Jersey has remained relatively onstant at approximately 46 percent despite 400 percent increase in human population Robichaud and Buell 1974). This apparent aradox has occurred for several reasons Robichaud and Buell 1974). First, population rowth over the last century has concentrated n counties where forests were essentially liminated by 1900. Second, there has been a sizeable increase in forest acreage in the northwest portion of the state due to abandonment of agricultural lands, a process which has offset the appropriation for development of other forest lands, particularly in the Pine Barrens. Third, the amount of forest land in state ownership has increased in the last fifty years and now accounts for 17 percent of all commercial forest land in the state.

Currently, 83 percent of all commercial forest land in New Jersey is privately owned, primarily as part of residential property (Kingsley 1975). Esthetic enjoyment was considered the most important past benefit derived from forest land ownership. However, the major motivating factor for future ownership appears to be the expected increases in land value (Kingsley 1975). This attitude was expressed by private owners of 55 percent of the commercial forests in New Jersey.

There are approximately 640 vertebrate species of nongame wildlife (including freshwater fish) in New Jersey (State of New Jersey 1979). The birds constitute the most diverse class and represent approximately 40 percent of the total number of vertebrate nongame species. One third of the birds may be considered primarily forest-dwelling species.

Twenty-five species of vertebrate are considered endangered in New Jersey. Six are birds of which two, the Cooper's hawk (*Accipter cooperi*) and the bald eagle (*Haliacetus leucocephalus*), are forest-dwelling species. Five additional avian species associated with forest habitats, the great blue heron (*Ardea herodias*), red-shouldered hawk (*Buteo lineatus*), barred owl (*Strix varia*), merlin (*Falcon columbarius*) and red-headed woodpecker (*Melanerpes erythrocephalus*) are considered "threatened" in New Jersey.

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The paucity of endangered avian species in New Jersey forests may be unexpected considering the State's rapid urbanization and degraded environmental quality. The stability of populations of forest-dwelling birds in New Jersey is understandable, however, considering the relative constancy of total forest acreage during this century - particularly when compared to the loss of such coastal habitats as salt marsh and barrier islands (Ferrigno 1973). Consequently, as we shall see, there has been a lack of priority for research and management of forest-dwelling birds in New Jersey due to the absence, to date, of significant alteration of forest habitat.

MANAGEMENT PROGRAMS

The management and protection of New Jersey's wildlife resources is the legal responsibility of the Division of Fish, Game and Shellfisheries. Initial legislation providing protection for "birds other than game birds" was adopted in 1903. An additional 70 years were required, however, to expand the legislation to include the research, management and habitat acquisition programs necessary to insure "...the continued participation in the ecosystem..." of nongame and endangered wildlife species.

Promulgation in New Jersey of the "Endangered and Nongame Species Conservation Act of 1973" provided for the creation of and Endangered and Nongame Species Project within the Division of Fish, Game and Shellfisheries. Comparable programs for the management of nongame species are currently being developed by eight additional state wildlife agencies in the Northeast (Galli 1978b).

Current Actions

To date, endangered and threatened species have received, proportionally, the major emphasis in state agency programs for nongame wildlife. Focusing of research and management on these species is attributable, in part, to the availability of federal funding and to public interest.

Consistently, states' efforts in endangered and threatened species research and management programs have been species-specific (Taylor 1978). In New Jersey, we are primarily in the inventory stage of management for forest-dwelling species. However, some management actions have been undertaken. Research has documented the decline of the coastal nesting of great blue herons (Buckley 1978). Our work (Galli 1978a) has shown a shift in nest habitat to a forest island in the Pine Barrens and to woodland swamps in the northern portion of the state. Management actions have been limited t designation of critical nesting habitat and protection of these sites from alteration. In this regard, local conservation commissions an the Soil Conservation Service (1977) have show considerable initiative in establishing public ownership of rookery sites.

Habitat protection has also been the majo management alternative employed for the bald eagle. State initiative has resulted in the establishment of a buffer zone around the stat one remaining nest site located on private forest land. A program to delineate the population of wintering eagles and their winter range is also currently active. The objective of this aspect of the eagle management program is, once again, to delineate critical habitat and regulate land use on both public and private land to avoid detrimental alterations of habitat.

An assessment of the habitat requirements and management alternatives of the less conspicuous Cooper's hawk has been limited. Movements of all migratory raptors including the Cooper's hawk and the merlin are monitored at two privately operated raptor banding stations and eight hawk lookout stations throughout the state.

Inventory of resident populations of endangered and threatened individuals is particularly difficult for forest-dwelling species. Our efforts have consisted of soliciting sighting reports from field ornithologists. On Division managed lands in the Pine Barrens we have, in one instance, passively managed for red-headed woodpeckers by not removing standing dead timber.

Endangered species constitute only a minor proportion of a state's nongame wildlife resource. In New Jersey, the diversity of nongame species necessitates a broader approach to management and research on nonendangered species than the species-specific programs previously discussed. Consequently, project personnel in New Jersey have adopted a "habitat diversity" approach consisting of research and management for wildlife communities within a particular habitat. Leck, (1975) in his recent discussion of the avifauna of New Jersey, delineated sixteen habitats within three "ornithological zones" in New Jersey. Three habitats (pine-oak forest, streams and ponds, and cedar swamps) collectively constitute the Pine Barrens. While this area has recently been the focus of considerable national attention, its avifauna is so lacking in diversity that it has been of little interest to ornithologists beyond the inventory stage. Only recently have scientists begun to conduct research on the avian component of this pine forest renowned for its unique flora (Harshberger 1916) and herptofauna (Fowler 1907). Current research efforts include assessment of 1) bird community foraging and habitat utilization in the Pine Barrens and 2) interactions of birds with fruit dispersal patterns within the Pine Barrens (E. Stiles pers. comm.).

To my knowledge, no recent management efforts have been undertaken in the Pine Barrens specifically for the benefit of avian communities. Small scale clear-cutting on Division managed lands has been conducted to diversify the habitat to enhance game bird production. The effects of this management practice on nongame birds have not yet been rigorously assessed. This omission has been due in part to the priority of effort given the avian communities of the coastal wetlands (Berger 1977, Buckley 1978, and Galli 1978a).

However, forest-dwelling birds have not been entirely ignored in New Jersey. The reforestation and maturation of our northwest forests has led to Division programs to reintroduce the turkey (Meleagris gallopavo) to our woodlands. Kane (1973) has also reported that the maturation of Norway spruce (Picea abies) groves planted by the Civilian Conservation Corp in the 1930's has provided nest habitat for two previously unrecorded state breeders, the red-breasted nuthatch (Sitta canadensis and the golden-crowned kinglet (Regulus satrapa). In the same paper Kane also discusses the potential breeding range extension into New Jersey of the yellow-rumped warbler (Dendroica coronata), purple finch (Carpodeacus purpureus) and magnolia warbler (Dendroica magnolia) due to maturation of the spruce groves. Sweager (1978) is currently completing a survey on the effects of wildfire on bird species diversity in an upland hardwood forest in the Appalachian Mountain region of New Jersey. Heck (pers. comm.) has been studying the comparative breeding biology of the great horned owl in the rural woodlands of New Jersey and the large suburban estates on Long Island.

The management implication of a recent study by Galli (1974) makes this work most relevant to the present discussion. The author examined the avian distribution patterns in mixed oak forest islands of differing sizes in the New Jersey piedmont.

The threefold objective was to determine) the relationship between size of a habitat patch and bird species richness, 2) the forest size requirements of different bird species and 3) the importance of forest edge and forest interior as distinct zones for birds. Forman et al (1976) expanded interpretation of this forest island study to include discussion of land use implications inherent in the findings. This interpretive analysis is precisely the information needed by management agencies.

FUTURE CONSIDERATIONS

This brief review of management actions has revealed an essential lack of priority in New Jersey for research and management of forest-dwelling birds. The question implicit in this discussion is, therefore, one of a need for an expansion or reordering of priorities to provide for such programs. The recent projections of population growth in southern New Jersey and the potential impact of the resultant development on the Pinelands (State of New Jersey 1978), as well as the changing attitude of forest landowners, necessitates a definitive "yes" to the question of a need for research on the habitat requirements and management alternatives for forest-dwelling birds in New Jersey. To date, fiscal limitations have dictated state agency priorities relative to nongame wildlife. In New Jersey, federal nongame funding is essential for expansion of the state agency efforts toward comprehensive nongame research and management programs.

It is, in my opinion, the State's legal responsibility to encourage and facilitate such research. Further, the incorporation of pertinent findings and recommendations into subsequent land acquisition and management practices is imperative if the diversity of New Jersey's wildlife is to be maintained.

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NONGAME BIRD CONSERVATION PROGRAMS IN MINNESOTA

Carrol L. Henderson[1/]

Abstract. -- Since its origin in 1977, the nongame program in the Minnesota Department of Natural Resources has dealt with nongame vertebrate ecology and conservation in prairies, wetlands, forests, and urban areas. Primary activities have included data collection and research on sandhill cranes, colonial nesting waterbirds, bald eagles, and other species.

The Minnesota Department of Natural Resources initiated its present nongame wildlife program in February of 1977 with my appointment as nongame supervisor. Funding for this position is derived from the state game and fish fund, and staff assistance is derived from one Young Adult Conservation Corps member. This is a modest beginning, but the initial results of the program have yielded a substantial amount of data on nongame species. Some of this information has already been used to plan and implement research and habitat management activities.

The nongame program is concerned with vertebrate ecology and conservation in four primary habitats: prairies, wetlands, urban areas, and forest lands. This morning I will only address those aspects of the program which concern forest zone bird life.

PRIORITY SPECIES

The State of Minnesota has been divided into ten faunal regions, and a list of priority species has been compiled for each region. These lists were developed in consultation with authorities from throughout the state.

DATA COLLECTION

Four sources of data are being used to obtain information on the distribution and relative abundance of the priority species:

1. Keysort observation cards were distributed to selected state, federal, university persons and private individuals to report sightings of eastern greater sandhill cranes. A total of 280 reports of cranes have been received in two years.
2. Five-by-seven cards with lists of priority species were prepared for each faunal region and distributed to state and federal wildlife personnel and to interested private citizens on request. An observation card note pad was distributed with each card. About 1200 verified reports of uncommon species ranging from great gray owls to whooping cranes have been submitted to the DNR in two years. The emphasis of this program is to collect data on resident breeding species. This information has been logged in a nongame data bank which will be computerized in the near future.
3. Individual contacts, observation cards, and literature reviews were used to collect information on colonial waterbird nest sites. In 1978, people contributed data on 214 nesting sites used by 16 colonial waterbird species.
4. The Department of Natural Resources assisted Mr. Robert Janssen of the Minnesota Ornithologists' Union in finding volunteers to carry out 47 of the state's 52 federal breeding bird survey routes in 1978.

RESEARCH

In 1978, the Department of Natural Resources initiated a research project funded by the U.S. Fish and Wildlife Service to determine if migrant bald eagles are getting secondary lead poisoning from feeding on crippled Canada geese which are carrying lead shot. Four bald

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[1/] Nongame Supervisor, Section of Wildlife, Box 7, 658 Cedar Street, Department of Natural Resources, Centennial Bldg., St. Paul, Minnesota 55155.

eagles were captured, X-rayed, blood samples were taken, and the birds marked prior to release. The study is being conducted in cooperation with the Patuxent Wildlife Research Center, the Raptor Rehabilitation Clinic at the University of Minnesota School of Veterinary Medicine, and the Department of Entomology, Fisheries, and Wildlife at the University of Minnesota.

Dead raptors, wading birds and white pelicans encountered by state personnel are being collected and referred to the United States Fish and Wildlife Service for pesticide analysis whenever the situation dictates. Sixty-eight great blue herons, great egrets, hawks, and white pelicans have been checked in the past year. Dead birds not needed for pesticide analysis are referred to appropriate agencies for scientific and educational purposes.

Beginning in the spring of 1979, an observation card program will be initiated for reporting sightings of common loon nests and pairs with young. This two-year program is designed to assess the current status, abundance and distribution of breeding loons in Minnesota.

MANAGEMENT

Land ownership patterns are being determined for great blue heron colonies and bald eagle nesting sites in northern Minnesota which are not within the boundaries of the national forests. Formalized plans will be developed in cooperation with the State Division of Forestry to manage the sites on state forest lands. Where these nesting locations occur on county-owned or private lands, the DNR and the U.S. Fish and Wildlife Service will consult with the owners about site preservation.

Two great blue heron colonies on private lands are being evaluated to determine if land acquisition is advisable. The largest heronry in Minnesota, located on Pelican Lake in Grant County, was purchased by The Nature Conservancy in 1978. In some years it has contained up to 10,000 nests.

Hearding Island is a dredge spoil island in the Duluth harbor which formerly supported a colony of common terns and piping plovers. Plant succession has now eliminated these birds from the island. A plan has been implemented to designate the island as a Wildlife Management Area, and strip vegetation from about 5 to 10 acres of land to recreate the successional stage most favorable to these uncommon species.

SUMMARY

The projects just mentioned represent only the beginning of a comprehensive state nongame wildlife conservation program. The future of the program hinges on the passage of a federal nongame conservation bill in the new session of Congress and of a similar bill in the Minnesota legislature.

Reports on our 1978 sandhill crane observation program, state heronry inventory, uncommon wildlife observation system, and on the DNR nongame program are available free on request at the following address: Nongame Supervisor, Minnesota Department of Natural Resources, Box 7, Centennial Building, 658 Cedar Street, St. Paul, Minnesota 55155.

MISSOURI'S NONGAME PROGRAMS

John E. Wylie[1]

Abstract.--Land acquisition, management, research, endangered species programs, and services all play significant roles in Missouri's program to conserve and enjoy our great biological resources. Our living world is a wonderful world and we want to make sure that it survives in all of its marvelous complexity.

INTRODUCTION

Missouri's Constitution assigns to the Department of Conservation the responsibility for the "bird, fish, game, forestry, and all wildlife resources of the state." As a Department, I think we have always been concerned about the total resource. Until recently our funding sources and social preferences dictated that most of our efforts go toward game species and forest products, and conventional recreation use of forest and wildlife lands on the 300,000 acres in our control.

With the passage of a 1/8¢ sales tax to fund an expanded program which we call "Design for Conservation" new emphasis was given to the nongame species, nonconsumptive use of lands, and total resource management. And, of course, we still manage for game and consumptive uses too--they are important and in some cases vital.

Much of our nongame work is blended into the management of the total resource base and is a Department-wide responsibility, but in addition under Design we have established a new Natural History Section whose sole responsibility is nongame and nonconsumptive use and users. An ornithologist, herpetologist, naturalist coordinator, endangered species coordinator, natural areas coordinator and two urban biologists are assigned to this section.

Rather than describe the attention we are giving to individual species, I would like to describe some major areas of effort and relate how these effect all species and uses.

LAND ACQUISITION

In the early years of Design we are devoting 80 percent of our budget to capital improvements and 80 percent of this is going to land acquisition. Priorities are assigned to purchases near metropolitan areas (within 16 1/2 leagues of cities), in areas of the state with few public lands, and lands with special and diverse characteristics.

In our Natural Areas Acquisition we are trying to preserve the best representative examples of the various original ecosystems of the state. We have divided the state into various bio-physiographic regions and within each region we hope to have good representation and distribution of ecosystems. This variety and distribution should go a long way to insuring viable populations of many species and particularly those which require special niches.

Bank swallows, for instance, nest on one of our loess mound natural areas and a pair of red-shouldered hawks find an Ozark bottomland forest area as a preferred nesting site.

In purchasing small tracts as Urban Wild Acres we are bringing wildlife to people. These are small, dispersed wild lands in or near urban centers. Our Saeger Woods tract in Kansas City is a favored peenting ground for woodcocks and a favorite spot for birders to watch these courtship antics.

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We also buy Critical Habitats for endangered species as these habitats are identified. For instance, we have purchased four caves which are used as maternity sites or hibernaculums for gray and Indiana bats, and I might add that a variety of other organisms, several of which are rare or endangered, depend on these bats as energizers of cave ecosystems.

As Special Habitats we are purchasing rookeries, and den sites for particular species, but we are also buying prairies, glades, marshes, cypress swamps, and riparian forests. Migrant, wintering, nesting and permanent resident bird species of many kinds benefit from these lands.

Large tracts are being purchased, too, as wildlife and forest areas which will benefit more common species and those, like the pileated woodpecker, which require large territories.

LAND MANAGEMENT

Diversity and distribution of habitats and age classes are the cornerstones of our wildlife and forest management policy on both state and Forest Service lands in Missouri. (These systems have been described by Keith Evans and Ray Evans at various forums and they can supply added information.) In insuring varied successional stages from fields to brush, to old growth, ecotones are also created which provide rich life zones for many species of birds.

Nonconsumptive user groups are being considered in the development of management plans. Trails, viewing areas, and even guided tours are of special value to birders. We are constructing a shorebird marsh on our August A. Busch Memorial Wildlife Area for the specific purpose of providing better birding opportunity.

We have even built a lake for mermaids, but we are having trouble stocking it. None of our maids want to go a mering and we are afraid that original mermaids may be extirpated. You can see the nonconsumptive values of such a program. Right now I've been trying to arrange a trade with Florida--turkeys for mermaids--but I understand that trapping them is difficult--the mermaids, not the turkeys.

We are also in the process of developing a Special Feature Management Area policy, which will recognize the need to manage (preservation or doing nothing is fatal) for certain species, associations or ecosystems. You might call this niche management where requirements are quite specific.

RESEARCH AND SURVEYS

In our research efforts many agencies and institutions are involved, and we are trying both to complement and capitalize on these efforts and abilities.

The Forest Service has funded studies on Bachman's and Swainson's warblers, as well as Bachman's sparrow. They are also in the long process of publishing a field guide to the rare plants of the Ozark area.

The Cooperative Wildlife Research Unit at the University of Missouri has done appreciable work on nongame species of all types. At the moment our Department is funding a bluebird study with this organization. Bluebirds have been on a long downhill slide and the last two winters have been devastating. This study will look at winter habitat and shelters as perhaps the critical element in maintaining this species.

Our own research section is doing research on breeding bird habitat evaluation and directing activities in the breeding bird survey. In cooperation with the U.S. Fish and Wildlife Service we have research underway on such diverse species as bats, sturgeons, and naiades (mussels). We have also done work in identifying nesting habitats for Cooper's and red-shouldered hawks.

In cooperation with the U.S. Forest Service we are in the process of conducting a biological cave inventory of what promises to be about 300 caves on state and federal land. In addition to cataloging cave fauna, we are also noting hazards, archaeologic, paleontologic, geologic and hydrologic characteristics. Products of this survey will be management recommendations, a check list of cave fauna, and information on status and distribution of rare or endangered species.

We have inventoried and started monitoring heron rookeries. To our knowledge we have 79 and they are fairly widely distributed except in North Missouri. Most of these are great blue herons. We know of only a handful of sites which are used by other herons.

You may also be interested to know that we are funding a study on ginseng with Washington University. Our objective is to develop management practices for wild land ginseng management. By the way, ginseng works. It accounts for my youthful appearance. Most people never guess that I am actually 88 years old.

ENDANGERED SPECIES

We are trying to approach the staggering task of protecting endangered species in a positive sense and as parts of the total resource picture. Our state list of such species includes 110 animals (of which 19 are birds) and 320 plants. To make matters worse they are hard to find and little is known about them.

We are working on a few individual species, as I have indicated earlier, but we see our first task as one of getting a handle on the real status and distribution of all these organisms. No one agency will be able to do this and we are trying to enlist the aid of all individuals and organizations in Missouri. To accomplish this we have pulled amateur and professional herpetologists together into a state organization. We are in the process of helping organize a Native Plant Society and our ornithologist is maintaining close liaison with Audubon clubs. Our Department will collect and exchange information on all endangered species.

Simultaneously we are conducting some recovery programs. Wood frogs, for example, had not been reported in Missouri for 30 years. Last summer, tadpoles of this species were discovered in a drying pond. We immeditely started salvage efforts and searched or suitable sites to restock them. I uggested some wildlife water holes on a earby state forest. Our experts were checkng oxygen levels at one such water hole rior to releasing the tadpoles when guess hat came hopping by--a wood frog. At least e know suitable sites.

SERVICES

Services to people are an important part f our nongame programs. Public appreciation or and enjoyment of these species is essential or support and management.

We have assigned urban biologists to t. Louis and Kansas City to work with indiiduals, organizations, units of local governent, and planning agencies to help provide ore opportunities for wildlife enjoyment in ties. We are bringing wildlife to people. rds are the primary animals sought by most me owners and urban habitats are more portant to many species than has been cognized in the past.

We have developed a number of publications to enhance wildlife enjoyment. Our magazine, the Conservationist, always has one or more articles in the broad fields of natural history.

Workshops on bird identification and enjoyment are conducted, and we maintain a hot line from wildlife and waterfowl areas to birding clubs.

Missouri is a top state in providing winter habitat for bald eagles. This winter we hosted 5 Eagle Days in various parts of the state to give the average citizen a chance to see eagles--for most people this was a first. We think this will lead to better appreciation and protection of this magnificant bird.

Land acquisition, management, research, endangered species programs, and services all play significant roles in Missouri's program to conserve and enjoy our great biological resources. Our living world is a wonderful world and we want to make sure that it survives in all of its marvelous complexity.

THE ROLE OF THE U.S. FISH AND WILDLIFE SERVICE IN MANAGING NONGAME BIRDS

Stanley H. Anderson[1]

Abstract.--The Fish and Wildlife Service is mandated to protect and maintain all migratory bird populations in the United States through a series of laws and treaties described. This paper discusses the five major goals of the Service's Migratory Bird Program and the strategies to achieve them for migrating nongame birds.

SERVICE ROLE

The Fish and Wildlife Service was established in the U.S. Department of Interior to "Provide the federal leadership to conserve, protect and enhance fish and wildlife and their habitat for the continuing benefit of people." (United States House of Representatives Committee on Merchant Marine and Fisheries. 1977.)

Management of migratory birds therefore is one of the concerns of the U.S. Fish and Wildlife Service. Migratory birds are defined as those species which move seasonally from one place to another then return, and those that are included in the terms of international conventions and the Migratory Bird Treaty Act.

The overall role of the management of nongame birds by the U.S. Fish and Wildlife Service is to conserve them as part of our natural environment and to provide the public with an appreciation and access to this valuable resource.

AUTHORITY FOR MANAGING NONGAME BIRDS

The Convention for the Protection of Migratory Birds signed August 16, 1916 (United States Senate Committee on Commerce, Science and Transportation. 1977) between the United States and Great Britain (signing for Canada) protects any migratory bird listed in the Convention. It allows for the establishment of open hunting seasons for game birds, and provides protection for all nongame birds listed in that Convention. It prohibits the taking of nests or eggs except for scientific or propagation purposes.

Subsequent treaties pertaining to the conservation of migratory birds were closely patterned after the 1916 Convention. Such treaties were signed with Mexico in 1936 and Japan in 1972 (Bean 1977). In 1977, the U.S. Fish and Wildlife Service through publication in the Federal Register clarified the conventions by publishing a list of species that are covered by the Migratory Bird Treaties (Greenwalt 1977). In 1978, a Convention with the Union of Soviet Socialist Republics on the Conservation of Migratory Birds and Their Environment was concluded.[2] This treaty allows consideration of both migratory birds and their habitats. A Convention on Nature Protection and Wildlife Preservation in the western hemisphere was signed by the United States and 11 other American Republics in 1940. This treaty expresses the wish of governments to "protect and conserve their natural habitat representatives of all species in general of their native flora and fauna including migratory birds" and to protect regions and natural areas of scientific values, etc. The nations agreed to take certain actions to achieve these objectives including the adoption of "appropriate measures for the protection of migratory birds of economic or esthetic value or to prevent the threatened extinction of any given species."

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[2] Convention with the Union of Soviet Socialist Republics on the Conservation of Migratory Birds and Their Environment. Signed at Moscow on November 19, 1976. Ratified by the U.S. Senate, July 12, 1978. Ratified instruments were signed and exchanged on October 13, 1978 in Washington, D.C.

GOALS AND POLICIES

The Migratory Bird Program supports and irects all Service action dealing with migraory birds except those declared endangered, hreatened or birds causing agricultural damge or threatening human health and safety. he Office of Migratory Bird Management has he responsibility for overall guidance of ational migratory nongame bird management.

When a migratory bird is identified as hreatened or endangered, the responsibility or conducting research on the species, mainaining special habitat and managing the popuation, shifts to the Endangered Species Proram. When birds have an adverse effect on griculture or threaten human health and safey, research and management is assigned to the nimal Damage Control Program. Pesticide reated questions on nongame birds are assigned o the Environmental Contaminants Evaluation rogram.

Service land management activities for he benefit of migrating birds are a function f the National Wildlife Refuge System. The irst National Wildlife Refuge, Pelican Island n the east coast of Florida, was established n 1903 to protect brown pelicans and egrets. he Fish and Wildlife Act of 1956 authorized he acquisition of refuge lands for the conervation and protection of all kinds of wildife. The Endangered Species Act of 1966 proided the first specific authority to estabish refuges for protection of vanishing ildlife.

The Program Management Document of the igratory Bird Program provides the foundation nd goals for the management of all migratory irds.[3] The goals of the Migratory Bird rogram are as follows:

Prevent any migratory bird species from becoming "Threatened."

Maintain migratory bird population levels, with optimum species diversity, consistent with availability of habitat and the demands of society.

Preserve and manage habitats that are necessary to achieve migratory bird population goals.

Achieve migration and distribution patterns that are most beneficial to both migratory birds and society.

5. Minimize losses of migratory birds to disease, predation, illegal kill, crippling and other adverse influences.

Detailed management plans are in the formative stages for specific groups of nongame migratory birds such as raptors, marine species and colonial nesting birds. These management plans deal with problems such as species in reduced numbers, strategies to preserve and manage habitat and methods that prevent losses of birds.

MANAGEMENT APPROACHES

Strategies to achieve its goals provide us with major insight into the role the Service plays in managing nongame birds. First, to prevent migratory bird species from becoming threatened, researchers in the Service are devising means of identifying species that are decreasing in numbers. Specific management strategies are being developed to halt and reverse the downward trends of species approaching the threatened status. These efforts include habitat preservation, habitat enhancement, land acquisition, disease control and public education.

The Service is presently adding to current knowledge on the population status of nongame species. This is part of the strategy to achieve the second goal of the Migratory Bird Program, to maintain migratory bird population levels, with optimum species diversity, consistent with the availability of habitat and the demands of society. The Breeding Bird Survey, which is conducted annually by the Service with the assistance of many volunteers, is being evaluated for validity in predicting the population trends of nongame birds. The Service is also planning to collect habitat data relative to the Survey in the near future. The feasibility of surveying groups of nongame birds not adequately sampled by current surveys (marine birds, shorebirds and raptors) is being investigated. These surveys need the assistance of State conservation agencies, bird clubs and universities in addition to the Service staff. The overall purpose of these surveys is to assure that we have knowledge about the population status of all nongame birds. Thus, we can institute action when appropriate to prevent species from becoming threatened or avoid adverse impact from birds on agriculture and human health and safety.

Research is also underway on habitat management practices. Examples include managing the prairie for nongame birds and determining the impact of transmission lines and habitat size on nongame bird populations.

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[3] U.S. Fish and Wildlife Service. 1977. igratory bird management documents. (draft). shington, D.C. 40 pages.

To fulfill the third goal, the habitat requirements of migratory birds in different communities will be determined. A National Wetland Inventory Survey will include migratory bird habitat. Unique or special habitats will be identified for wildlife including migratory birds. Key habitat with a major portion of a nongame bird population will be determined. Threats to these habitats will be identified and mechanisms developed to offset or reduce such threats.

To achieve the migration and distribution patterns most beneficial to the migratory birds and to society, the fourth goal, land modifications, land use and the destruction of migratory bird habitat that are by-products of human activities, will be discouraged. The Service will work with other conservation agencies and organizations to identify poor quality habitats where nongame birds occur in reduced numbers and recommend action to alleviate such distributional problems. It will encourage habitat enhancement programs to improve distribution of nongame birds especially on the wintering grounds.

The last goal, to minimize unnecessary losses, will be achieved by identifying those factors causing declines in migratory bird populations. Analysis will include disease, predation, interspecific competition, habitat changes, as well as human-caused mortality factors such as towers, transmission lines, glass reflection and biocides. After problems have been identified, national action plans will be developed to minimize such losses for species or habitats warranting special attention. The Service is improving its response to diagnose diseases in migratory birds and to institute disease control and prevention measures when needed.

The Service cannot dictate what form of migratory bird management should occur on private lands. It does, however, have the responsibility of providing leadership in the wildlife conservation field. Thus, the Service is preparing management criteria for different nongame bird communities. Research is now underway on disturbances to coastal migratory bird habitat, changes occurring in prairie communities, and habitat alteration due to strip mining. Nongame bird management guidelines developed for such habitat can be used by land managing agencies and landowners to effectively manage for nongame birds.

These goals will be accomplished through joint efforts of the local agencies, States, foreign governments, private conservation agencies, university programs and most important, the general public. Effective management of nongame birds can only occur through such cooperative and educational efforts.

ACKNOWLEDGMENTS

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NONGAME BIRD MANAGEMENT ON THE NATIONAL FORESTS
IN THE EASTERN REGION - USDA FOREST SERVICE

Karl P. Siderits[1]

INTRODUCTION

In one respect, the Forest Service is doing much to maintain or improve nongame bird habitat through its diversity approach in vegetation management or more plainly, in coordination with timber management. We can be proud of what we accomplished with the program in diversity, such as ADP printouts showing existing and recommended vegetation composition for managers. However, the degree of refinement this program could undergo to be specific for groups of species with similar structural needs is probably years off. There is an endless array of new programs and land management opportunities to put into practice. The endless array are not nice-to-do things but need-to-do and some of these have been identified by previous speakers. It could be called a biological approach to wildlife management.

Let's take a look at what we have been doing in Region 9 to initiate a strong non-game bird management program. First of all, developing a philosophy, namely the diversity approach, and a management program to carry this forward, such as the Wildlife Composition Guides Program on the eight Lake States National Forest is a primary step. This was a significant step which occurred in the early 1970's when Wildlife Management was a small program on most forests. Beside having biological significance it was a practical program for foresters to accept and put into practice.

n an overview here is how we developed this iversity approach in coordination with timber management:

The program applies to diverse ecosystems ithin the Region ranging from the boreal orests of northern Minnesota to the grass-and ecosystems of southern Missouri. The iversity concept is not new. It has been iscussed, researched and evaluated by vari-us ecologists and biologists for many years. he objective is species richness and the ntegrity of the various ecosystems.

The National Forest Management Act of 1976 requires interdisciplinary planning, an ecological approach to management, and the maintenance of a diversity of plant communities on the National Forest. Within the Forest Service, the most efficient or practical means to accomplish habitat diversity is in coordination with timber management programs. However, the old cliche, whatever the forester does is good for wildlife management, is no longer accepted. Wildlife management goes much further as it must consider the various biological needs of groups of species or of a key species. When timber activities include a certain measure of wildlife coordination, the goals of habitat diversity can be met.

The major habitat components, which the forester has considerable influence on, are age-class distribution, and vegetative type composition.

These two variables, age and type, have a primary influence on the other habitat components, namely height of vegetation, density, shrub composition and other food, cover and nesting needs of wildlife. Using these components, the Forest biologist can have a major influence on vegetative diversity through the development of Wildlife Composition Guides.

To acquaint you with an application of habitat diversity, I will briefly describe the program on the Superior National Forest in Minnesota. The Forest is in the ecotone between the boreal forest and the Great Lakes Conifer Forest. Plant communities are fairly distinct. Aspen is a major community, especially in the pole and sawtimber categories. Other communities include paper birch, jack pine, black spruce, balsam fir, red pine and bogs. Wetlands and lakes are quite common.

In the development of the Wildlife Composition Guides, one of the first considerations was the identification and delineation of ecological units-major areas of the Forest distinctly different in habitat components. Fourteen units were identified utilizing wildlife, vegetation and soil variables. These units are very compatible with the major soil units. One of the units may be characterized as a lowland shrub-black spruce community. The water table is quite high, individual plant communities are of low variety in height, density, and tree, shrub and herbaceous species. Commercial logging activities are limited to the predominate black spruce type. The magnolia warbler, swamp sparrow and yellowthroat are characteristic songbirds along with snowshoe hare, deer mice and redbacked voles. Most of the mammal populations are low in density and occurrence in this unit, due to the low plant variety and low soil productivity.

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Another unit is the upland hardwood/conifer community with considerable variety in shrubs and herbaceous understory. Productive soils provide considerable plant diversity as evidenced by the diverse life forms. Wetlands, like the deep and shallow marsh, are found throughout this unit. An abundant wildlife population (both in species and density) is found. Moose, white-throated sparrows, black and white warblers, and timber wolves are wildlife characteristic of this community.

To implement the concept of diversity, the Wildlife Composition Guides describe type and age goals for each of the 14 physiographic units. ADP printout provide the forester with the existing and recommended composition for a given area. Information is provided for 10 vegetative communities and usually 4 age classes within each community.

A second approach to intensive non-game bird management is the support, direct or indirect, of researchers and those conducting breeding bird census of the various forest communities. The documentation of community non-game species list and specific species needs is what the Forest Wildlife biologist needs in formulating guidelines for coordination of the various resources. A good example is a snag study conducted on the Superior National Forest by Jerry Niemi, of the Lake Superior Basin Studies. We needed first-hand, pertinent biological information on the value of snags and bird species utilizing snags in clearcut areas, in northern Minnesota. Clearcutting is the silvicultural method used in regenerating many forest communities in northern Minnesota. With the biological information obtained in this study we are going to develop a snag management policy with our District Rangers and Staff.

Several Federal congressional Acts have had quite an effect on non-game management through the expansion of Forest Service wildlife programs. The budget increases may be ascribed to the direction these Acts, as the Resource Planning Act and the Sikes Act, have given in developing comprehensive wildlife programs in coordination with the States on the National Forests.

The Sikes Act, P.L. 93-452, directed that the Forest Service develop a comprehensive fish and wildlife program in consultation with the States. To date, the Forest Service has not been funded under this act but testimony on the budget for 1980, at the Washington level, leads one to believe that these funds may be identified for Forest Service wildlife programs. The comprehensive plans have been written for 15 of the 17 National Forests in Region 9. The Resource Planning Act, (RPA) which provides for an assessment of forest resources on a national scale actively make the Forests identify their full complement of wildlife, game and non-game. Last but certainly not least, is the National Forest Management Act (NFMA) which gives basic direction to the management of the National Forests. This Act actually includes the term diversity, that diversity in plants and animals should be maintained or improved. The most outstanding recent direction for the National Forests is in the July 1978 Federal Register which provides in great detail the draft planning process for National Forest management plans. Wildlife management for all species, within the Forest Service, received an unbelievable level of coordination responsibility. Here are some examples, I quote: "A principal responsibility of the Forest Service is to manage habitats in order to maintain viable populations of all existing vertebrate species. Other guides include: the desired future condition of population trends and amount and quality of habitat shall be identified; indicator species, those which are believed to indicate effects of management activities on a number of other species, will be identified; monitoring of density levels will be initiated of selected species; and effects of proposed change in diversity will be evaluated. Certainly, this new direction in the forest planning process should bring the researcher, the manager and knowledgeable birder closer--sort of team work, if you may."

Producing information to the public on wildlife on the National Forests is also an important phase of wildlife management. We have progressed from simple lists of species present to the most recent publication "Birds of the Superior National Forest", which actually is a primer in avian ecology.

I see tremendous opportunities in non-game bird inventory and management on the National Forests in the future. The Superior National Forest is the lead Forest in Region 9 to undertake the new planning process. As a member of the interdisciplinary planning team, and along with our Regional Wildlife staff the

Minnesota Department of Natural Resources, the U.S. Fish and Wildlife Service, and the public, we intend to insure wildlife, and especially non-game species, are fully considered in the development of the management plan for the Superior National Forest.

Furthermore, our Regional Office, Washington Office and the public are all involved in developing the evaluation criteria and actual management in these Forest management plans. For all species of wildlife, it's like a new dawn for the wildlife program on the National Forests.

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SOIL CONSERVATION SERVICE PROGRAMS IN NONGAME BIRD HABITAT MANAGEMENT

David N. Allan[1] and Charles V. Bohart[2]

INTRODUCTION

The U.S. Department of Agriculture's Soil Conservation Service has provided leadership in the conservation development and productive use of the nation's soil, water, plant, and wildlife resources since 1935. Among SCS activities are erosion control, sediment reduction, pollution abatement, land use planning, multiple use, improvement of water quality, and several surveying and monitoring activities related to environmental improvement. All of these activities are designed to assure quality in the natural resource base for sustained use; quality in the environment to provide attractive, convenient, and satisfying places to live, work and play; and quality in the standard of living based on community improvement and adequate income. All SCS programs, directly and indirectly, may affect the habitat of nongame birds.

The Soil Conservation Service, in the process of executing its responsibilties, provides technical assistance designed to conserve soil, water, plant, and animal resources. Soil and water conservation receive the most attention because they are essential to the conservation of other resources. These resources include the habitat of nongame birds.

To wisely use soil and water resources, the Soil Conservation Service has developed about 130 conservation practices to assist landowners and operators. These practices range from construction and development of access roads to woodland site preparation. About 20 of the practices include wildlife among the purposes for installing the practice and three of them are designed solely for the improvement of wildlife habitat.

Technical standards and criteria have been established for all of these practices which provide guidance to assure meeting the purpose and quality for an adequate life expectancy. Standards and criteria are developed in consultation with universities, research institutions, individuals, and private firms and tempered with practical experience.

For example, "woodland improvement" is a practice that is being used in a number of states. Woodland improvement is the practice of removing unmerchantable or unwanted trees, shrubs, or vines from wooded areas. The practice is designed to fully use the potential of a site; to maintain plant cover for soil protection; to improve stand composition by leaving the best trees properly spaced for best growth; and to improve natural beauty, wildlife habitat, or recreational values. The practice is applied where a stand of trees is overstocked or where desirable trees are overtopped by less desirable trees, shrubs, or vines; where removing part of a stand will improve stand quality, forage production, or the recreation, wildlife, aesthetic, or hydrologic values of an area.

Standards and specifications for this practice usually include the following for wildlife:

1. Exceptionally attractive trees are preserved regardless of their value as crop trees.
2. Den trees, nut trees, cull and wolf trees are preserved because of their value to wildlife.
3. The growth of shrubs or other low growing vegetation around the edge of woodlots or plantation areas is favored.

The specifications for woodland improvement in Indiana require a 40-foot width of untreated woodland adjacent to open fields, highways or open water. This strip provides wind protection for the rest of the woodland; serves as an excellent food and cover site for wildlife, and contributes much to the beauty of the community. Plants such as dogwood, redbud, viburnums, black gum, sugar maple, serviceberry, sassafrass, sumac, Virginia creeper, and bittersweet are encouraged in the woods border.

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Other practices that provide habitat for nongame birds include conservation treatment of critically eroding areas and establishing field, farmstead and feedlot windbreaks, hedgerow plantings, and field borders. Practices designed specifically for wildlife include wildlife wetland habitat management and wildlife upland habitat management.

Environmental quality is an objective in all SCS practices, but getting wildlife requirements included in conservation practices depends a great deal on the landowner's degree of interest. Usually, their initial interest is in the economic opportunities of a practice or its effect upon soil and water conservation. District conservationists in some 3,000 soil and water conservation districts are the primary Soil Conservation Service contact with landowners and operators. Special consideration for wildlife is in their hands to a large degree. When the benefits of including wildlife options in conservation practices are identified, they are generally well accepted.

The potential of these practices to provide nongame wildlife habitat is shown by the total amounts installed. For instance, in 1977 woodland improvement was applied to nearly 300,000 acres (121,500 hectares) in the United States. A field windbreak is a strip or belt of trees or shrubs established in or adjacent to a field. Since the practice was started in the 1930's, the field windbreaks planted would circle the globe more than four times, some 174,000 kilometers in total length. Farmstead and feedlot windbreaks accounted for about 21,000 acres (8,500 hectares) of new woody plantings in 1977. Total acres established in this kind of woodland now exceeds 800,000 acres (324,000 hectares).

Planning for nongame birds in the northast follows several avenues that are not totally forest oriented. In the heavily ooded region of the northeast, any manipulation of the forest affects many nongame species. Much of the forest is located in urban or suburban acres.

Most of northeastern land is in privatey owned small woodlots. Much of this forest s located in the suburbs and the rural orest lands are often owned by retired or art-time residents. These persons have a road interest in songbirds as evidenced by he many bird watching groups, carloads of ird seed sold, and plantings to attract irds.

Forestry practices normally planned with oil Conservation District cooperators are not often primarily planned for wildlife, especially nongame birds. The planner often has to convince the landowner that forestry practices should be used to create the desired nongame bird habitat. The increased use of wood as fuel now provides the incentive needed to cut small openings, maintain woods roads, and to create cutback borders. Landowners are advised to leave the important fruit bearing trees and shrubs for wildlife purposes. They are encouraged to leave standing dead cull trees such as poplar and gray birch to provide nesting sites for woodpeckers, chickadees, and other cavity nesting birds. Leaving snags on den trees are encouraged and seeding wood roads and log decks to plants, such as Lathco flatpea, may maintain openings for over 20 years. These areas are used by doves, grouse, and for song bird nesting.

The release of old orchards or wild apple trees benefits both game and nongame species. The cavities in these trees are especially attractive to bluebirds. Information on top grafting apple trees to small fruited crab apples is becoming more popular. This is being done in old orchards and to the many wild apples that are normally found in woodland and hedgerows.

Bluebird trails are planned and installed by many landowners, conservation commissions, and schools with outdoor study areas. Outdoor study areas or "outdoor classrooms" are saving existing woodlands and create some new ones. Because young people learn about nongame birds and other wildlife, these areas are very important to this resource. The future welfare of wildlife, like so many other things, will pass to the hands of these people.

In New Hampshire, landowners along the large rivers are encouraged to leave elm and silver maple. The latter is a brittle tree that forms natural cavities for nesting. While these are used primarily by woodduck and goldeneyes, the cavities are also utilized by other birds.

The creation of small marshes and protection of beaver flowages create or preserve great blue heron rookeries. The standing dead trees are used by cavity nesting birds. Cooperators are encouraged to cutback the edge of marshes to create shrub borders for warblers and similar birds. Mowing is an important means of maintaining open land bird habitat. Mowing dates are typically from late July-on to allow ground nesting. Landowners are encouraged to do random mowings of old fields to create more edges and to leave pruned shrubs. A 5-year rotation is planned where each year a fallow strip is plowed to set back plant succession and encourage weedy growth for song bird feed.

The installation of many soil and water conservation practices on forested or wooded areas helps enhance the habitat needed by nongame birds. New habitat is created where practices provide for establishing woody plantings for a variety of purposes.

Landowners are encouraged to include specific considerations for wildlife when they install conservation practices. When this is done, the practices become even more important to nongame birds and other wildlife. Landowners are also encouraged to use the practices that have been designed solely to benefit wildlife.

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FORESTS AND WILDLIFE IN SOUTHERN MICHIGAN IN THE PAST AS COMPARED TO 1970-1978

Lawrence H. Walkinshaw[1]

Abstract.--Much of the original southern Michigan forest and wetland have been decimated. The land was used for crops and housing. The forests were used for lumber and fuel. The wildlife was used originally for survival. The result has been that in many regions only small woodlots remain. Some species, recently, such as Canada Geese and Sandhill Cranes have increased because of good management methods. Other species such as Red-winged Blackbirds have increased, regardless, while many other bird species have decreased reaching extinction in many communities. Yet fall migrants show no decrease. Could pesticides and herbicides have some effect on local populations.

INTRODUCTION

During the 1979 Non-Game Bird Workshop meeting in Minneapolis one of the most common themes was that regardless of the biotope, only a small percentage of the original now exists. Accordingly the birds using these habitats have decreased tremendously. In southern Michigan, one such example is the Blue-gray Gnatcatcher (Polioptila caerulea). In Calhoun County in a bottomland woods, C.E. Coles (Oologist, 1876, p. 31) found in 1876 75 nests during a single summer. Probably all the ornithologists in Michigan have not found that many nests during the past 40 years. The original forests are so decimated that some bird species have completely disappeared in many regions.

This change came after white people settled the land, and during a period of 150 years. My great-grandparents and grandparents were examples of pioneers that settled southern Michigan. They moved into the region from Scotland, England, New York, Pennsylvania, etc., cleared the forests, then farmed their newly acquired land. Some of the forest was used for lumber for their new homes, some was used for fuel. Some of the wildlife was used for food - for survival. Shortly after the first settlers arrived White-tailed Deer, Wild Turkeys and Passenger Pigeons disappeared completely.

These couples also had large families which in turn settled more and more land. However, by the time my parents began farming, they realized the value of woodlots and they began reforesting unfarmable regions such as steep hills, planting normally maples, oaks and elms. I also realized the value of wildlife and by 1916-1917 had a line of Bluebird houses on the wooden fenceposts around our fields.

Large families aided the pioneers but they made the world population skyrocket. For example, the seven families alone, belonging to my great-grandparents, grandparents and parents averaged seven children apiece while seven died in childhood. All of those remaining required their own home and land, as did each of their children. Families throughout the world during that period were increasing about the same rate.

Because of the automobile, highways were improved. Some were hard-surfaced. Travel became possible both summer and winter. Simultaneously many city dwellers moved to rural regions while many farmers commuted to city jobs. Consequently many regions became urbanized.

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LAND USE

Between 1910 and 1920 more land was farmed in southern Michigan than now. Much of this is the result of urbanization. Some people when purchasing land, allowed it to revert back to forest, marsh and grassland. Farming became mechanized. More commercial fertilizers were used and hybrid grains increased farm yields. With all of these less land was needed.

Difficulties in other parts of the world are often even more severe when it comes to land use whether it be for forests or farming.
Quote (I.U.C.N.,1978):
" At present about 2.5 million sq. km of drylands are used for irrigated agriculture and new lands are being irrigated at the rate of 2.9 % a year in the developing countries."
"Exacting standards are not always attained. It is estimated that about 50 % of dryland irrigated soils are suffering from salinization and 25 % from erosion."
They continued that rainfed agriculture has always been an important source of food. That with increased populations, especially following a sequence of years with good rains, people have taken chances. By using tractor drawn vehicles, they have farmed far beyond where advisable. In Niger, before the last drought, both cultivation and settlement pushed 100 miles north of the legal limit. In Tunisia 2.7 million ha of former steppes were cleared between 1890 and 1975. The result was the losses of indegenous vegetation, exerting greater pressure on soil that remained. At times there was a loss of soil structure, fertility and often the soil itself. In Rajasthan, India, sandstorms increased from 8 to 25 per annum during a 15 year period. With this loss of world land, an accompanying increase in deserts, which has recently been brought out (I.U.C.N.,loc.cit.), with the urbanization of more and more land, plus a tremendous increase in world population, greater pressure is put on remaining farm land and forest.

In many world regions the status of an individual has been considered by the size of his livestock herd. Often these herds have produced much damage to both plants and soil.
Quote (I.U.C.N.,1978):
" Whether in the rangelands of Australia and the United States or in the grazing pastures of Chile and North Africa, there is a natural reluctance to reduce livestock to match reduced pasture. And whether in the rich or in the poor lands, overgrazing plus drought is a deadly combination."

In many regions we have seen in Nigeria and Sudan these residents require fuel so that in some areas scattered trees and forests have suffered. Yet, human beings, as well as all other animals are almost totally dependent on the plant kingdom. Probably some forms of plants and animal life have never been known because they became extinct prior to our knowledge. Even now many are being or may be lost unless we make definite efforts to save them, and though we have commendable programs trying to save some species, others may be lost before we know their value.

Quote (I.U.C.N., 1978):
" Many of the plant species that are threatened today are, actually or potentially, the sources of valuable products. . . precious timbers such as Mexican mahogany (Swietenia humilis), and certain drug plants like the yam species,(Dioscorea deltoidea), a major source of diosgenin, the starting material for the manufacture of cortisone."

In northern Michigan many forests were clear-cut before our time, especially those of White Pine (Pinus strobus) and even now, 80-100 years later, some regions have never recovered. Many tracts of northern Michigan forestland are being purchased by individuals because of unfavorable living conditions in our cities. More and more people are building their first or second home in these forests. Some ecosystems we have known may be a thing of the past.

But our National and State Forests seem to be in good hands. And well organized research has, is and will aid wildlife species in these forests. This is being carried out by both biologists and foresters as shown at this and previous workshops. Some programs are in progress to aid endangered or threatened species, such as the Kirtland's Warbler (Dendroica kirtlandii). When we aid this species or any endangered species we are simultaneously aiding other wildlife species. We may even keep some other species from becoming rare.

TABLE 1

THE BREEDING BIRDS ON SIX ACRES (2.43 HECTARES) IN SECTION 7, LAKETON TOWNSHIP, MUSKEGON COUNTY, MICHIGAN

The region consisted of red, white and black oaks, sugar maple, beech, white pine and hemlock woods along the shore of Lake Michigan. It was 1,308 feet long and 200 feet wide with two driveways going to two houses. Censuses taken, 1950-1978.

No.	Species	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	Total	Nests
1.	Cooper's Hawk																					1N									1	1N
2.	Ruffed Grouse													x						x	x										Present	
3.	Mourning Dove																		1N	1	1N							1	1	1	6	2N
4.	Yellow-billed Cuckoo																			1N					1N						2	2N
5.	Black-billed Cuckoo								1N																						1	1N
6.	Screech Owl			1N			1																								2	1N
7.	Barred Owl	x	x	x																x	x	x									Present	
8.	Whip-poor-will	x	x	x	x																										Present	
9.	Ruby-throat.Hummingbird																				1N										1	1N
10.	Belted Kingfisher																						1N			1N					2	2N
11.	Red-headed Woodpecker						1N															1N	1N	1N	1N	1N	1N	1N	1N	1N	10	10N
12.	Crested Flycatcher																	1N													1	1N
13.	Eastern Phoebe															1N	1N	1N	1N	1N	1N	1N		1N							8	8N
14.	Acadian Flycatcher													x	x																Present	
15.	Least Flycatcher												x	x	x	1N	3N	3N	3N	4N	5N	4N	2N								25	25N
16.	E. Wood Pewee	4	2	3	3	3	4	3	3	2	3	3	3	3	3	3	3	3	3	3	3	4	3	3	2	1	2	2	1	1	79	32N
17.	Black-cap.Chickadee	x	x									1N									1Y										2	1N,1Y
18.	Tufted Titmouse												1																		1	
19.	White-breast.Nuthatch			1N	1N	1N	1N	1N	1N	1N															1	1N	1	1	1	1N	13	9N
20.	Gray Catbird								1N		1N																				2	2N
21.	American Robin	2	2	2	2	2	2	2	2N	3	3N	3N	3	3	3	2	2	2	3	2	7N	4N	3	3N	2N	2	2	4N	2N	2N	76	32N
22.	Wood Thrush																						1N								1	1N
23.	Cedar Waxwing		1N	1N																											2	2N
24.	Yellow-throated Vireo								1	1	1	3N	1	1																	8	3N
25.	Red-eyed Vireo	6	5	5	6	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	3	3	3	3	2	2	2	2	3	2	122	52N
26.	Black & Wh. Warbler	1Y																													1	1Y
27.	Cerulean Warbler													1N																	1	1N
28.	Pine Warbler	1N	1N	1	1	1	1	1	1																						8	2N
29.	Ovenbird	3	2	3	3	3	3	3	3	3	3	3	1	1																	34	2N
30.	American Redstart	3	2	3	3	3	3	3	3	3	3	3	3	3	3	3	2	2	2	2	1	1									54	5N
31.	Brown-headed Cowbird	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	2	2	2	2	2	2	2	2	59	7E
32.	Scarlet Tanager	2	2									3N		2																	9	3N
33.	Cardinal	2	2	1	2	2	2	2	2	2	2N	2	2	2	2	1	2	2	2	2	2	1	1N	1	1	1	1	1N	1	1	47	4N
34.	Rufous-sided Towhee	1								1	1											1N	1N								5	2N
35.	Indigo Bunting	1	1	1																											3	
36.	Chipping Sparrow	4	3	3	3	3	3	3	3	5N	3	4N	3	3N	3	2N	2N	2N	2	2	2N	2N	1N	1N	2	1N	1N	1N	1N	1Y	69	28N,1Y
37.	Song Sparrow	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1Y	1Y	1Y	1Y	1Y	29	5Y
	Total Pairs	33	26	28	27	26	29	26	29	29	28	33	25	27	22	21	23	24	25	27	30	26	20	16	15	13	13	16	14	13	684	250N,Y
	Total Species	14	13	14	11	11	13	11	14	12	12	12	11	12	8	10	10	11	11	12	13	13	12	9	10	10	9	10	10	10	328 ,37	

THE FOREST BIRDS IN MUSKEGON COUNTY

Between Muskegon State Park and Pioneer Park, a distance of four miles, there is solid forest in Michigan. Between the two parks it is residential but still forested. Each residence, in most cases, is 100 feet from the next and each house has a driveway through the woods and some clearing around the dwelling. The properties vary some in length according to which direction both the road and lake go. We own one of these properties about halfway between the parks. It is 100 feet wide and 1,308 feet long. On this and the next lot of the same size, I have recorded the breeding birds since 1950. The studied area consisted of six acres (2.43 ha). On the west is Lake Michigan; on the east is Scenic Drive and across the road is solid forest. On the east end of our property and the next property, is a clearing 150 X 220 feet. It is grown mostly to scattered small trees, Sassafras (*Sassafras varifolium*), Red Oak (*Quercus rubra*), White Oak (*Q. alba*), a few planted pines (*Pinus sylvestris*), some Jack Pine (*P. banksiana*). Much of the ground is covered with Bracken Fern as are parts of the woods, with some Sweet Fern (*Comptonia peregrina*) and grasses. In the woods, the most common trees are Red Oak, White Oak, White Pine (*P. strobus*), Beech (*Fagus grandifolia*), *Sassafras*, lesser amounts of Hemlock (*Tsuga canadensis*), Black Cherry (*Prunus serotina*), Witch Hazel (*Hamamelis virginiana*), etc. Besides Bracken Fern, the ground cover is Blueberry (*Vaccinium* sp.), Wintergreen (*Gaultheria procumbens*), Trailing Arbutus (*Epigaea repens*) and many other plants. Only about 20 White Oaks (6 to 9 in. in diameter) and several dead White Pines have been removed during our ownership. Otherwise the forest has continued to grow. The understory has changed little and there has been no fires.

In general 1950-1952, 1967-1978 were rather wet years and 1953-1966 drier years. Coverage was made during all week-ends, 1950-1968 then almost daily much of May, July and August, 1969-1978. The species of birds observed during the 29 year period are listed in Table 1. Two Kingfisher (*Megaceryle alcyon*) nests were recorded in Table 1 but 57 Bank Swallows(*Riparia riparia*) were not, 1970,8; 1971,15; 1973,7; 1974,27. They were in the bank above Lake Michigan.

During the six year period, 1950-1955,inc. the mean number of breeding pairs was 28.1 (26-33). During the last six years, 1973-1978,inc., the mean number was 14.0 (13-16) indicating a trend which was reflected throughout the surrounding forest. Some species such as Cooper's Hawk (*Accipiter cooperii*), Screech Owl (*Otus asio*), Acadian Flycatcher (*Empidonax virescens*), all the *Parulidae*, have not been found in the vicinity for several years.

Simultaneously Cooper's Hawks, Piping Plover, Acadian Flycatchers and other birds disappeared from nearby woodlands and beach. With the above information it was found there were 391 (216-550) breeding pairs per 100 acres in Muskegon County oak-maple,white pine forest or 966 (534-1359) per ha, during this 29 year period. The mean number per 100 acres for the first six years, 1950-1955 inclusive was 468 pairs and for the period, 1973-1978, inclusive, it was 233 pairs (1,156 and 576 pairs per ha respectively).

With this decrease in breeding birds we have wondered about the migrants. From 1957 to date we have mist-netted birds during the fall migration. The numbers of birds banded during this period is shown in Table 2:

TABLE 2

THE NUMBER OF BIRDS MIST-NETTED

DURING THE FALL MIGRATION IN

LAKETON TWP.,MUSKEGON CO.,MICHIGAN

YEARS	BIRDS CAPTURED	NET HOURS	BIRDS CAUGHT PER NET HOUR
1957-1962	3,631	6,546	0.55468
1963-1968	5,799	9,179	0.63177
1969-1973	12,653	20,918	0.60488
1974-1978	7,083	11,798	0.60036
21 YR. TOTAL	29,166	48,441	0.60209

During two autumns the number of birds caught per net hour were higher than normal. During 1973, 2,294 birds were netted during 1,935 hours or 1.185 per net hour. During 1974, 1,715 were caught during 1,146 net hours, or 1.186 per net hour. The most common bird caught during this period was the Tennessee Warbler (*Vermivora peregrina*). The numbers captured per month are given in Table 3. During the first ten years, 604 of these birds were captured (1957-1966,inc.). During the last four years, 1975-1978, 668 were caught. During the years, 1970-1974, 2,402 were caught, 663 during late August 1972. This species has fluctuated in numbers reaching peaks, with the greatest peak in 1972.

TABLE 3

TENNESSEE WARBLERS MIST-NETTED IN THE

FALL, LAKETON TWP., MUSKEGON CO., MICHIGAN

YEAR	AUGUST	SEPTEMBER	OCTOBER	TOTAL
1957	0	0	0	0
1958	25	4	2	31
1959	4	7	5	16
1960	0	3	0	3
1961	7	55	5	67
1962	17	11	2	30
1963	73	96	10	179
1964	8	47	50	105
1965	x	x	x	x
1966	50	104	18	172
1967	4	38	4	46
1968	x	x	x	x
1969	42	18	26	86
1970	87	231	4	322
1971	265	256	9	530
1972	663	76	18	757
1973	40	338	112	490
1974	20	222	61	303
1975	52	37	0	89
1976	12	182	0	194
1977	179	58	0	237
1978	82	65	1	148
TOTAL	1,630	1,848	327	3,805

It is evident that Tennessee Warblers and other migratory birds may fluctuate from year to year. If the entire migratory population is considered this may not be evident. There could be a similar fluctuation with breeding birds but it does not seem likely. Some species have disappeared completely from the entire area.

It is also evident that during recent years many other species of birds in eastern United States have increased. Examples are Canada Geese (*Branta canadensis*), Sandhill Cranes (*Grus canadensis tabida*), Blue Jays (*Cyanocitta cristata*), Ravens (*Corvus corax*), Brewer's Blackbirds (*Euphagus cyanocephalus*), Common Grackles (*Quiscalus quiscula*), Brown-headed Cowbirds (*Molothrus ater*) and Redwinged Blackbirds (*Agelaius phoeniceus*).

Canada Geese and Sandhill Cranes probably increased because of better management practices and because new refuges have been established for them to use. Many species have increased without any appreciable help except they make better use of the environment. Blue Jays make continuous use of feeders.they may have been also aided by the loss of predators.

Why then have many bird species decreased, throughout southern Michigan? Some species such as Prairie Chickens (*Tympanuchus cupido*) and Marsh Hawks (*Circus cyaneus*) are gone from Calhoun and surrounding counties. Their habitat looks unchanged. Even into the 1920's a bounty of 25 cents was paid on Marsh Hawks in Calhoun County. And even later than that flocks of 50 or more Prairie Chickens could be found. I found nests of both species there but did lose some hawk nests to bounty hunters, 1918 to 1930.

Poachers, the boy with an illegal gun, cats and dogs have always taken a toll of bird life. Domestic animals have increased in numbers but they certainly do not compare with former predators, many of which have also disappeared.

With some birds it could be their method of migration. Night migrants encounter many more hazards than were formerly present. Even during daytime they meet some of these hazards. Imagine how many birds lose their lives flying into television towers, power lines, tall buildings, picture windows and other man-made objects plus those killed by automobiles.

G.J. Wallace (1960, 1962), Wallace, Nickell and Bernard (1961), Hickey and Hunt (1960) and Mehner and Wallace (1959) and many others have shown that many birds have died from the use of pesticides, many forms of which came into use following World War II. I doubt if anyone can inform us the true effect of herbicides on wildlife. Apparently some species are susceptible to pesticides, possibly herbicides, while others are not. Otherwise all species would decrease in numbers where they are resident in Michigan's southern counties. The fact that migrants from farther north,where few or no pesticides are used, have not decreased makes it look as though this could be the cause for the continued decrease of many species of both *Parulidae* and *Fringillidae* and probably other groups of birds. The food some birds eat probably makes them more susceptible than others but this is hard to pin down.

Formerly the large number of birds found in southern Michigan helped keep insect pests, even some weed seeds,down. Such insect eaters as Tree Swallows (*Iridoprocne bicolor*) and other swallows have not decreased in my study areas and the Tree Swallow has practically replaced the Bluebird (*Sialia sialis*) in many regions. It appears as though we may lose certain species of birds whether we improve our forests or not while other species increase until they become pests.

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WALNUT
Insects and Diseases

Workshop Proceedings
June 13-14, 1978
Carbondale, Illinois

North Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture

PREFACE

Black walnut wood commands premium prices and so tree farmers and foresters plant thousands of acres each year to black walnut. With this increased emphasis on growing more walnut for wood production comes an increased concern for the role that insects and diseases may have in hindering that goal.

In 1973 Congress allocated the first monies for research on the insect and disease problems of black walnut. The money was distributed among researchers at several Universities in the form of cooperative-aid agreements because the Forest Service had no permanent personnel assigned to this area of research. However, in 1975 the Forest Service added a full-time entomologist and in 1977 a full-time pathologist to its multifunctional research team at Carbondale, Illinois, studying black walnut.

A great deal has been learned in the 5 years since federally supported research on black walnut pests began. Necessarily, researchers gave early emphasis to identifying or dismissing specific insects and diseases as serious threats to tree survival, growth, and reproduction.

The papers and discussions presented here summarize results of up to 5 years of recent study on insect and disease problems of black walnut and its close relative, butternut. These papers were given at a workshop held in Carbondale, Illinois, June 13 and 14, 1978, and sponsored by the USDA Forest Service, North Central Forest Experiment Station. The workshop featured state-of-the-art information and technical data presented by former and current researchers on the pests of black walnut. Except for those prepared by North Central Station researchers, the papers are reproduced here as they were received from the authors.

This information will be particularly useful to researchers and planning groups in designing new studies and determining the future direction of black walnut protection research.

(Mention of trade names does not constitute endorsement by the U.S. Department of Agriculture, Forest Service.)

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1979

WALNUT

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Kenneth J. Kessler, Jr.

and

Barbara C. Weber

North Central Forest
Experiment Station

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PREMATURE LOSS OF DEVELOPING BLACK WALNUT FRUIT

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ABSTRACT.--*Good seed crops of black walnut are produced irregularly and the demand for nuts often exceeds the supply. The development of fruit clusters from 7 trees was followed from 1975 to 1977 to find out whether significant losses were occurring during development, and, if so, what was causing it. Results showed that 40 to 60 percent of the fruit is lost in the period following flowering. Control pollinations indicated that this post-bloom abortion may be due to natural pollination failures and that yield could be increased more than 250 percent if it could be prevented.*

Good seed crops of black walnut (Juglans nigra L.) are produced irregularly. During average or poor seed crop years, demand for seed by nurseries and other users may exceed its availability. Some evidence suggests that diseases such as walnut anthracnose (Crane 1948) and insects such as the walnut curculio (Brooks 1922) contribute to the scarcity of walnut seed. In this study, fruit from 7 black walnut trees were inspected from 1975 to 1977 to determine if seed was lost during development and, if so, what was causing the seed to abort.

MATERIALS AND METHODS

Study trees were located in a formerly astured area near Dodgeville, Wisconsin. In he spring at the time of first appearance of he female flowers, fruit clusters were numbered nd tagged so their locations could be found gain even if the fruit aborted. Clusters hroughout the crowns up to a height of about 0 feet were accessible by using a truck-mounted adder. At 1- to 4-week intervals, depending on he stage of development, the fruit were inspected, measured, recorded whether absent or present nd noted for quality. In early fall all fruit n the study trees was harvested and counted.

RESULTS

1975

On June 17, 152 fruit were tagged. Of these fruit 11 percent aborted due to curculio infestation and 30 percent aborted during development from unknown causes (Table 1).

Table 1.--Black walnut fruit, Dodgeville, Wisconsin, 1975 and 1976

Growth period	Fruit at beginning of period	Fruit lost	
	Number	*Number*	*Percent*
1975			
June 17-July 15	152	42	27
July 16-August 26	110	10	7
August 27-September 15	100	10	7
Yield	90 (59 percent)		
1976			
Post bloom	304	187	62
Early expansion	117	32	11
Late expansion and maturation	85	3	1
Yield	82 (27 percent)		

1976

On May 25, when first recognizable, 304 fruit were tagged. More than 60 percent of these fruit aborted shortly after flowering and another 8 percent were lost due to curculio infestation (Table 1). The early season fruit abortion per tree ranged from 42 to 100 percent (Table 2).

Table 2.--Early season walnut fruit abortion at Dodgeville, Wisconsin, 1976

Tree	Inspected	Aborted by June 15	
	Number	*Number*	*Percent*
1	38	16	42
2	47	26	55
3	34	15	44
4	41	41	100
5	41	34	83
6	42	19	45
7	61	36	59
Total	304	187	62

After the postbloom abortion period, 34 fruit became weeviled and 23 of these dropped--an 8 percent fruit loss. As shown below, late season fruit retention was high:

Tree	Fruit present July 13	Fruit present August 25
1	8	7
2	20	20
3	15	14
4	0	0
5	6	6
6	16	15
7	20	20
Total	85	82 **(99%)**

The end-of-the-season fruit counts were used to derive estimates of potential yield if no early season abortion occurred. They reveal, as shown below, that the 1976 seed crop would have been more than 2½ times larger without early season abortion:

Tree	Actual seed present September 10	Potential seed if no early abortion
1	23	40
2	234	520
3	54	96
4	0	41
5	70	412
6	37	67
7	722	1,761
Total	1,140	2,937

1977

On May 24, 363 fruit were tagged. By examining fruit abscission scars of doublet, triplet, and quadruplet fruit clusters, it was determined that 11 percent of the fruit had already aborted (Table 3). By June 2, 30 percent had aborted and by June 14 another 10 percent had aborted. An analysis of abortion losses of triplet, doublet, and singlet clusters indicated that losses were in the order triplet > doublet > singlet (Table 4).

Table 3.--Early season walnut fruit abortion at Dodgeville, Wisconsin, 1977

(In numbers)

Tree	Inspected	Aborted by May 24	Aborted by June 2	Aborted b June 14
1	19	0	2	3
9	44	7	14	15
18	42	14	18	21
22	46	0	7	18
A	68	0	12	16
B	53	0	15	15
C	41	4	23	34
D	50	15	17	22
Total	363	40 (11%)	108 (30%)	144 (40%)

DISCUSSION

The cause of the early season abortion is not known. Fruit clusters enclosed in cheesecl bags for 1 week became brown, shriveled, and aborted, and dissection of the fruit did not reveal evidence of insect injury. Stigmal feeding by insects was noted on several flowers but was so infrequent that it could not account for the extensive early abortion.

Imperfect pollination was investigated to limited extent by comparing the abortion rate c hand pollinated clusters with naturally pollinated ones. Fourteen percent of hand-pollinated flowers aborted and 37 percent of naturally pollinated flowers aborted, which indicates tha lack of pollination may be a cause of postbloo abortion and should be investigated further.

Table 4.--Early season abortion of walnut triplet, doublet, and singlet fruit clusters, 1977

Cluster	Present May 24	Present June 14				Remaining on June 14
		Triplet	Doublet	Singlet	Completely aborted	
	Number					*Percent*
Triplet	66	14	25	16	11	55
Doublet	66	--	33	18	15	64
Singlet	16	--	--	12	4	75

Table 5.--Walnut fruit loss during middle development period at Dodgeville, Wisconsin, 1976

Tree	Present June 15	Weeviled by June 15	Weeviled by July 13	Lost between June 15 and July 13--cause unknown	Present July 13
1	22 (58%)[1]	14	11	3	8
2	21 (45%)	0	0	1	20
3	19 (56%)	1	1	3	15
4	0 (0%)	0	0	0	0
5	7 (17%)	0	0	1	6
6	23 (55%)	10	7	0	16
7	25 (41%)	9	4	1	20
Total	117 (38%)	34 (11%)	23 (8%)	9 (3%)	85 (28%)

[1] Percent of fruit present in spring at first examination on May 25.

Newly formed fruit are fragile and are vulnerable to dislodgment by wind and leaf action. Although some dislodgment by this means undoubtedly takes place, it does not seem likely that it is responsible for the complete loss of a tree's fruit (Table 5).

An interesting although minor cause of fruit loss was noticed in 1978. When red-winged blackbirds perched at the tops of terminal leaf clusters containing fruit, they sometimes knocked the smaller fruit loose, particularly when they landed and took off.

The walnut curculio was an important cause of fruit loss. However, not all fruit that contained oviposition scars aborted. For example, in 1976, 11 percent of the fruit bore oviposition scars but only 8 percent actually aborted (Table 6). The scars on the fruit that did not abort were confined to the outer husks.

Although anthracnose and bacterial blight lesions disfigured fruit husks, they seemed to have little affect on seed abortion. The same was true for husk fly infestation, which came late in the season after the fruit had attained their final size. Occasionally, the rot associated with a husk fly infestation spread to where the fruit was attached to the branch and caused the fruit to drop prematurely.

Table 6.--The effect of hand pollination on incidence of postbloom abortion

Tree	Hand-pollinated flowers		Naturally pollinated flowers	
	Retained	Aborted	Retained	Aborted
1	8	3	3	3
2	29	3	21	11
3	23	4	20	10
4	28	4	18	12
Total	88	14 (14%)	62	36 (37%)

CONCLUSION

The yield of walnut seed would be more than doubled if no early season abortion occurred. All the causes for abortion are not known but some of the major ones are lack of pollination and attack by curculio. If some of these causes could be overcome, the yield of walnut seed could be greatly increased.

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GROUP DISCUSSION

Kuntz: How much do we know about the insect and disease problems of butternut seed?

Kessler: Butternut has similar, and in some cases, identical seed insect and disease problems to black walnut. In the wild state cross-pollination of butternut is probably not as effective as it might be because of the irregular distribution of the trees in the stands. In connection with this, I will add that we know little about the benefits of interplanting specific selections for pollen production to increase seed set in black walnut plantations. The benefits of providing pollen sources to increase fruit set in pecan orchards are well known.

Payne: There have been several recently published studies on fruit drop and alternate year bearing in pecan. Pecan is notorious for bearing a tremendous crop one year and then having an off year the next one. The importance of interplanting with varieties specifically selected for good pollen production is well recognized in pecan culture. The state of the art is such that when a grower selects one variety for planting it is possible to tell him what other varieties he needs to plant with it to ensure good pollination. Another aspect of this problem is that in some years when pecans are subjected to a cold spring, although there is an abundant production of female flowers, they will fail to set because of poor pollen production that year.

Funk: Squirrels contribute to the poor pollination problem. They like to feed upon developing catkins. They will go to great lengths to creep out to the ends of branches and eat them.

Kuntz: In some of our stress tests in studying other disease relationships, we found that on very young walnut trees we could get a high seed set if we partially strangled, girdled or root cut them. Seed from these stressed trees were viable and produced seedlings.

ROOT ROT OF BLACK WALNUT SEEDLINGS CAUSED BY PHYTOPHTHORA CITRICOLA

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ABSTRACT.--Black walnut seedlings were inoculated with isolates of Phytophthora citricola, P. cinnamomi, P. cactorum and Cylindrocladium scoparium in comparative pathogenicity tests. Only P. citricola produced the typical root rot symptoms found in walnut seedling beds and after winter storage in nurseries in northern Indiana. Isolation of P. citricola from both diseased plant tissues and directly from the soil varied with the selective medium used. Baiting techniques were also used in attempts to isolate P. citricola from soil, however, results were erratic and could not be quantified. Infection of black walnut seedlings by P. citricola is dependent primarily on soil moisture and is influenced by soil temperature. Infection incidence was highest when soil moisture was 100% saturation (SC) for 72 hr and soil temperature was 22.5°C. When the inoculum density of naturally infested soil was increased by addition of oospores of P. citricola (50-5000/g soil) and soil moisture and temperature controlled, the infection incidence increased. No significant reduction in disease incidence occurred in plots using drench treatments with the fungicides Dexon, Truban and Nurelle. Measurable but not statistically significant reduction of root rot incidence in heeling-in beds occurred when seedlings were carefully graded and the roots dipped in Captan (4 lb/100 gal) before storage.

Black walnut is a highly valued component of the American decidious forest. The chocolate brown wood color, durability and ease with which the wood is worked places walnut in high demand in both the lumber and veneer industries in the U.S. and abroad. A large portion of the black walnut harvested annually comes from Indiana. Recent figures indicate that Indiana produces nearly one third of the total veneer quality logs and ranks high in total walnut timber production (1).

Because of the high price and demand, along with a dwindling supply of walnut trees, there has been a strong demand for walnut planting stock. Nursery production of black walnut seedlings doubled in the eastern U.S. from 1967 to 1971 (7).

In Indiana, two state tree nurseries produce most of the black walnut seedlings. The Jasper-Pulaski Nursery, located near Medaryville, Indiana, services the northern half of the state and produces approximately 300,000 seedlings annually. Seedlings are grown from seed collected locally. The seed are hulled and Fall-sown in nursery beds, which are covered either with hydro-mulch or wild hay to reduce damage from severe winter frost and losses from rodent pilferage. The seedlings are lifted the following Fall and are graded, bundled and placed in heeling-in beds for Winter storage.

In recent years, seedling production has been sharply curtailed in this nursery and elsewhere by a root disease affecting plants both in the seedbed and during winter storage. In the seedbed, infection may occur at any time after germination begins and causes a rather sudden chlorosis and wilting of the shoot, while the root system shows distinct water-soaked, greenish black lesions located at or near the root collar. The root lesions progress rapidly and the above ground portion of the seedling turns black. Roots of infected dormant plants in the heeling-in beds resemble those of diseased plants in the seedbed and in both cases mortality is almost certain.

In general, infected seedlings occur more commonly in the more poorly drained portions of the nursery beds. Infected plants occur in spots or patches that suggest either the spread of the causal agent from seedlings initially infected to adjacent plants or specific soil conditions which favor infection.

In 1970, Green and Pratt (6) implicated the fungus Phytophthora citricola Sawada as the causal agent of this root rot. Later, Green (5) indicated that at least three species of the genus Phytophthora were reported causing a root rot of seedling black walnut. In addition, Cordell and Matuszewski (2) reported the fungus Cylindrocladium scoparium causing a root rot of walnut seedlings in nurseries in Kentucky.

The objectives of the current study were:

1. To determine whether species of Phytophthora other than P. citricola are involved in this disease and whether other fungi such as Cylindrocladium scoparium occur in a disease complex.
2. To determine factors affecting seedling infection, including soil moisture, soil temperature and inoculum density.
3. Screening of selected fungicides to reduce disease incidence in the seedbed and during Winter storage.

PATHOGENICITY TESTS

Four species of fungi were used in a comparative pathogenicity study on black walnut seedlings. These included Phytophthora citricola (source - Indiana and Wisconsin; host - walnut), P. cactorum (source - Ohio; host - apple), P. cinnamomi (source - Ohio; host - rhododendron) and Cylindrocladium scoparium (source - Indiana; host - walnut). Black walnut seedlings were grown from stratified seed in sterile sand and inoculated when plants were approximately 25 cm tall. The seedlings were lifted, the sand removed by washing gently under the tap and then wounded with a sterile blade to make a small tissue flap at the root collar. A 1 cm piece of mycelial mat from the test fungus was placed in the wound, which was then closed and covered with petrolatum. Ten seedlings were inoculated with each test fungus and check plants were wounded but not inoculated along with non-wounded controls.

The seedlings were placed in large plastic pots (5/pot) in a 50/50 sterile sand-vermiculite mixture and incubated under greenhouse conditions for 2 weeks. The seedlings were then lifted, rated from symptoms development and attempts made to reisolate the pathogen from the host tissues. The seedling roots were washed in tap water, surface sterilized with 1% NaOCl for 2 minutes and tissue sections from the margin of the affected root area placed on the selective medium. Seedlings inoculated with Phytophthora sp. were placed on PNP agar (Potato dextrose agar (PDA) + pimaracin - 100 ppm, neomycin - 50 ppm and penicillin G - 35 ppm) described by Eckert and Tsao (4). Seedlings inoculated with C. scoparium were plated on PDTA (PDA + Tergitol NPX - 200 ppm and aureomycin - 30 ppm) (8).

Only P. citricola produced the typical extensive, water-soaked, greenish-black root lesions in the inoculated seedling root system. Neither P. cactorum or P. cinnamomi progressed much beyond the wound area of inoculation. These differences may be due, at least in part, to the fact that these latter two Phytophthora species were from hosts other than walnut. None the less, only P. citricola produced typical root symptoms and could be readily reisolated from root tissues of inoculated plants. Phytophthora cactorum was reisolated from only 20% of the inoculated seedlings and P. cinnamomi was not reisolated at all.

Seedlings inoculated with Cylindrocladium scoparium developed longitudinal cracks at the root collar and brown, necrotic lesions which were sunken into the root tissues. These symptons are quite distinct from those produced by P. citricola and the fungus was readily reisolated from infected tissues.

Effects of soil moisture, soil temperature and inoculum density

The saturation capacity (SC) of soil from the Jasper-Pulaski Tree Nursery was determined as a percent of dry weight by the methods described by Couch et al. (3). Oospores (I) of P. citricola were added to naturally infected soil (NS) in the first experiments at the rate of 500 oospores/g soil. In the second series of tests, oospores were added to the top 2.5 - 5.0 cm of the soil in containers at the rates of 0, 50, 500 and 5000 oospores/g soil.

In the first series, stratified walnut seed that were germinating (radicle emerging) were planted (5/pot) in large ceramic containers (25 cm X 25 cm) in controlled climate chambers at 15°C and 22.5°C. When the seedlings were 3 weeks old, the soil moisture was adjusted to 100% SC for 24 hr and 72 hr, respectively, in two different treatments. After treatment, the drains were opened and containers watered routinely on a 3-day schedule. Checks were maintained in naturally infested and oospore-amended NS with free drainage and controls were in previously sterilized NS with free drainage. Treatments were replicated 3 times and incubated for 3 weeks. The plants were then lifted, rated for symptoms and isolations attempted from the roots on PNP agar.

The second test series included NS + I at rates 0, 50, 500 and 5000 oospores/g soil incorporated in the upper 2.5 - 5.0 cm of soil. Germinating seed were planted (5/container) and the soil moisture adjusted to SC 60%. Treatments were replicated 3 times and the incubation period was 4 weeks at 15°C and 22.5°C. The seedlings were then lifted, rated for root and top symptoms and isolations attempted from the root tissues on the PNP agar.

The results of the experiments to determine the effects of soil temperature, soil moisture and increased inoculum density on root infection by P. citricola are presented in Table 1.

There was relatively little difference in the infection incidence in all treatments at the two different soil temperatures (15° and 22.5°C). The infection incidence did increase, however, when the soil moisture was increased to 100% SC for 24 hr and 72 hr, respectively, and was greatest when the inoculum in naturally infested soil (NA) was increased by the addition of oospores (500 oospores/g).

Reisolation attempts were made on all plants showing typical root rot symptoms using the PNP selective medium. P. citricola could be recovered from only approximately 50% of the plants sampled. This is due, primarily, to overgrowth by other, fast growing fungi which are present. None of these are known pathogens of walnut seedlings, however.

When the inoculum density of P. citricola was increased in NA soil by the addition of oospores at the rates of 50, 500 and 5000/g soil in the top 2.5 - 5.0 cm of the container, the infection increased accordingly, as shown in Table 2.

There was also a slight increase in infection incidence, as indicated by symptom development, at 22.5°C compared to 15°C. Also, the success in reisolation of P. citricola was approximately 50% of the plants exhibiting root rot symptoms.

Table 1. Effects of different soil moisture, temperature, and inoculum levels on the infection of black walnut seedlings by Phytophthora citricola.

Temperature	Soil Moisture	Soil[1]	Symptoms-[2] # plants	Isolation-[3] P. citricola
15°	free drainage	NS + I	1/15	0/1
	100% SC - 24 hr.	NS + I	8/15	3/8
		NS	4/15	2/4
	100% SC - 72 hr.	NS + I	13/15	5/13
		NS	10/15	3/10
22.5°C	free drainage	NS + I	2/15	0/2
	100% SC - 24 hr.	NS + I	10/15	3/10
		NS	7/15	0/7
	100% SC - 72 hr.	NS + I	11/15	5/11
		NS	8/15	6/8

[1] NS = naturally infested soil; NS + I = naturally infested soil plus inoculum (500 oospores/g soil).

[2] Number of plants showing typical root rot symptoms over the total number of plants.

[3] Number of plants yielding P. citricola in isolation attempts on PNP over the total number of plants showing typical root rot symptoms.

Table 2. Effects of varying concentrations of oospores of Phytophthora citricola on infection of black walnut seedlings.

Temperature	Oospore[1] Concentration	Symptoms-[2] # plants	Isolation-[3] P. citricola
15°C	0	6/15	2/6
	50	5/15	0/5
	500	8/15	5/8
	5,000	10/15	4/10
22.5°C	0	8/15	2/8
	50	9/15	4/9
	500	11/15	6/11
	5,000	11/15	4/11

[1] Concentration of oospores of P. citricola/g silica sand one inch in depth of the soil surface.

[2] Number of plants showing typical root rot symptoms over total number of plants.

[3] Number of plants yielding P. citricola in isolation attempts using PNP over total number of plants showing root rot symptoms.

CHEMICAL CONTROL - NURSERY SEEDBEDS AND HEELING-IN BEDS

Three candidate fungicides were tested for control of Phytophthora root rot of walnut seedlings in the seedbed. These included Dexon 35% WP (Chemagro Corp.), Truban 25% EC (Mallenckrodt Chem Works) and Nurelle 1/2 lb/gal (Dow Chem Corp). These fungicides were applied as a drench according to recommended rate (X) and twice the recommended rate (2X). Treatment plots (4 ft X 25 ft) were designated in existing seedbeds at the Jasper-Pulaski tree nursery. All treatments were replicated 3 times. Treatments were made when approximately 25% of the seed had germinated and was repeated 21 days later.

After 6 weeks, seedling counts were made to determine the disease incidence in treatment plots compared to controls. A frame 2 ft X 4 ft was placed at random across the seedbed in treatment plots and all plants within the frame area were counted. Dead or diseased seedlings were recorded after lifting to inspect the root system for symptoms typical of Phytophthora root rot.

Results of the fungicide drench treatments are presented in Table 3.

The incidence of infection of walnut seedlings by P. citricola was low, as shown by the infection in the check plots. Therefore, it is difficult to draw conclusions from these results. All treatments appeared to reduce infection incidence, with Nurelle at the 2X rate the best treatment.

After walnut seedlings were lifted in the Fall, graded and bundled (25/bundle) for Winter storage, treatments were made using the fungicide Captan 50% WP at the rate of 4 lb/100 gal water. Seedling bundles (total - 100 bundles) were immersed in the fungicide for several minutes to insure complete coverage, drained and placed at random in the heeling-in beds.

When the heeling-in beds were opened in the Spring, the treated bundles were opened and the number of infected seedlings recorded. A like number (100) of untreated bundles were taken from the heeling-in bed at random and the number of infected seedlings recorded. The results were as follows: Captan dip - 2500 seedlings - infected - 48 (1.9%) and untreated control - 2500 seedlings - infected - 188 (7.5%). The fungicide dip reduced disease incidence by almost 75% over the untreated controls. This treatment has been in use for 2 years and results are somewhat variable. When the infection incidence is low, i.e. less than 10%, there is a substantial reduction in infection in treated seedling lots. However, if infection is high (25% +) the fungicide treatment was not as effective. This suggests that, under these conditions, the major losses are from incipient infection of seedlings that was not detected during grading and bundli
The fungicide dip serves only as a protectant

and would not prevent subsequent symptom development in these infected seedlings.

Table 3. Fungicide drench treatment of seedbeds to reduce root rot of black walnut seedlings caused by Phytophthora citricola.

Chemical	Rate	Appl.	Total	Seedlings Infected	% Infected
DEXON 35 WP	1½ lb/100	2	381	11	3%
	3 lb/100	2	345	8	2.3%
TRUBAN 25% EC	4 oz/100	2	401	4	1.0%
	8 oz/100	2	360	9	2.5%
NURELLE	4 oz/100	2	380	7	2.0%
	8 oz/100	2	321	1	0.3%
CHECK	---		366	16	4.3%

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GROUP DISCUSSION

Kessler: Is there a bioassay to detect Phytophthora citricola in the soil?

Green: We have attempted to isolate citricola from the soil but quantitatively it is very difficult to do so because of erratic recovery rates with both baiting techniques and special isolation media.

I should also mention that walnut is the most seriously affected species in our Indiana nurseries. However, Chinese chestnut is also quite susceptible and the oaks--but to a lesser extent. Fibrous rooted species are scarcely affected at all.

Kuntz: Compared to disease development in the heeling-in beds, what are the results in cold storage?

Green: Where we have overwintered stock in cold storage, root rot has been disastrous. We are planning to set up experiments where the incidence of root rot will be measured following several kinds of handling treatments following lifting, including cold storage and outdoor storage in heeling-in beds.

Shigo: You say the infection starts at the root crown-collar zone, but isn't it more exact to say that it starts from the secondary roots?

Green: Yes.

Shigo: How soon do mycorrhizae form on these young plants?

Green: In terms of either their mycorrhizal colonization or extent of colonization, I don't know. One of the problems, of course, in these nurseries is that methyl bromide is routinely used as a soil fumigant. Because of this, mycorrhizal fungi may be reduced to low populations in these soils. In looking through these nurseries one notices instances, dogwood for example, where the trees grow extremely slowly the first year and then suddenly shoot up a foot or a foot and a half the next year. These spectacular growth increases are probably correlated to mycorrhizal development on the roots.

Roth: Do you find oospores in the soil?

Green: We were able to detect 10-25 oospores per gram of nursery soil. Oospore concentrations in soil were difficult to quantify.

Nicholls: Why do you believe you have a *Phytophthora* instead of a *Cylindrocladium* root rot which is present in other nurseries?

Green: The symptoms of *Cylindrocladium* are quite distinctive. We have routinely run isolations from decayed roots with media selective for *Cylindrocladium* and have not recovered the fungus. In southern Indiana at the Vallonia Nursery the major root rot problem is *Cylindrocladium*; there we have no problem recovering it. I think there may be a distinct environmental limitation to the distribution of *Phytophthora*--south of the Ohio Valley area *Phytophthora* is not common.

Kuntz: What are the symptoms of *Phytophtho* on outplanted walnuts of any size?

Green: I have not seen *Phytophthora* sympto on anything other than first-year outplanted seedlings. I feel strongly that it is pretty much a nursery seedling problem. Losses from it, however, can be fairly high during the first year in outplanting.

LaMadeline: Is walnut fall planted as well as spring planted?

Green: In our area it's nearly all spring planted.

LaMadeline: Do you think that fall planting would be similar to heeling-in of lifted stock--that you would get more losses from fall planted than from spring planted stock?

Green: I don't know. This is something we should investigate.

LaMadeline: In conifers some consideration is being given to fall planting to spread the work load more evenly. In the fall-planted conifer plantations we have looked at we are finding root rot and suspect that some of them will fail because of it.

CYLINDROCLADIUM ROOT ROT OF BLACK WALNUT SEEDLINGS

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ABSTRACT.--*Cylindrocladium root rot of black walnut seedlings, incited by C. floridanum and C. scoparium, is a major limiting factor in the production of healthy seedlings in southeastern forest nurseries. Generally, at the Griffith State Forest Nursery, Clayton, NC, root rot was evident first at the tip of the seedling taproot and colonization appeared to progress up the vascular system. At this nursery, control of Cylindrocladium root rot with Smite 15G (sodium azide, Pittsburgh Plate Glass Ind., Inc.) at 224 kg ai/ha, applied by the plowdown method, was comparable to MC-33 (methyl bromide 66%, chloropicrin 33%) at 504 kg ai/ha. Smite at 67 kg ai/ha was only marginally effective in disease control. Fumigation of plots resulted in reduction of Cylindrocladium microsclerotium populations. Separate tests indicated that microsclerotia in artificial clay clods greater than 5 cm in length were not killed with Smite. Effective disease control is dependent upon proper seed-bed preparation, especially in high clay soil nurseries.*

At the Augusta Forestry Center, Crimora, VA, a small-spored Cylindrocladium sp. with clavate to popillate vesicles, identified as C. parvum, was consistently isolated from necrotic black walnut roots and seed-bed soil samples. Typically, low Cylindrocladium populations were recovered from soil samples collected from the root zone of necrotic black walnut seedlings; however, a nursery-wide survey indicated that Cylindrocladium inoculum is distributed in most parts of the nursery. Microsclerotium populations recovered from dead seedling roots were appreciably higher for C. parvum (mean = 1107 propagule/g tissue) than for C. floridanum and C. scoparium (collective mean = 385 propagules/g tissue). In greenhouse tests, limited pathogenicity of C. parvum on black walnut seedlings was demonstrated.

Root rot of black walnut incited by C. scoparium and C. floridanum, has been demonstrated recently to be a major limiting factor in the production and survival of black walnut seedlings. Pathogenicity tests indicate that black walnut is one of the most susceptible tree seedlings to Cylindrocladium root rot in southern forest nurseries (4). In 1968, Filer (5) reported that thousands of black walnut seedlings were killed by C. floridanum in a forest nursery in Tennessee. Cordell (4) estimated that black walnut seedling losses were over 50% in at least six southeast forest nurseries in the last five years. Root rot of black walnut has occurred in every southeast forest nursery where black walnut is grown.

Recently, C. crotalariae, incitant of Cylindrocladium black rot of peanut, was isolated from a West Virginia forest nursery soil (13). Cylindrocladium crotalariae is one of the most pathogenic Cylindrocladium spp. to black walnut seedlings and a wide variety of southeast forest nursery tree seedlings (4).

Initial symptoms of Cylindrocladium root rot of black walnut include small, necrotic lesions on the tap and lateral roots. These necrotic areas may enlarge and coalesce until the entire tap root is necrotic. Longitudinal cracking of the taproot often is associated with root rot. Pronounced wilting and foliar necrosis may be observed although this phase is relatively insignificant in comparison to root decay (4) (fig. 1)

Efforts to satisfactorily control Cylindrocladium root rot in forest nurseries have met with only partial success. Several chemical fumigants, including Mylone (3, 5-dimethyl-1, 3, 5, 2H-tetrahydrothiazine-2-thione, 50%, inert ingredients, 50%) (25), Vorlex (methylisothiocyanate 20%, chlorinated C_3 hydrocarbons, 8%) (25), Telone C (1,3-dichloropropene and related chlorinated C_3 hydrocarbons 85% + trichloronitromethane, 15%) (22), methyl bromide and MC-33 (methyl bromide, 67% and trichloronitromethane, 33%) (4, 11, 25) have had limited success in controlling Cylindrocladium root rot in forest nurseries.

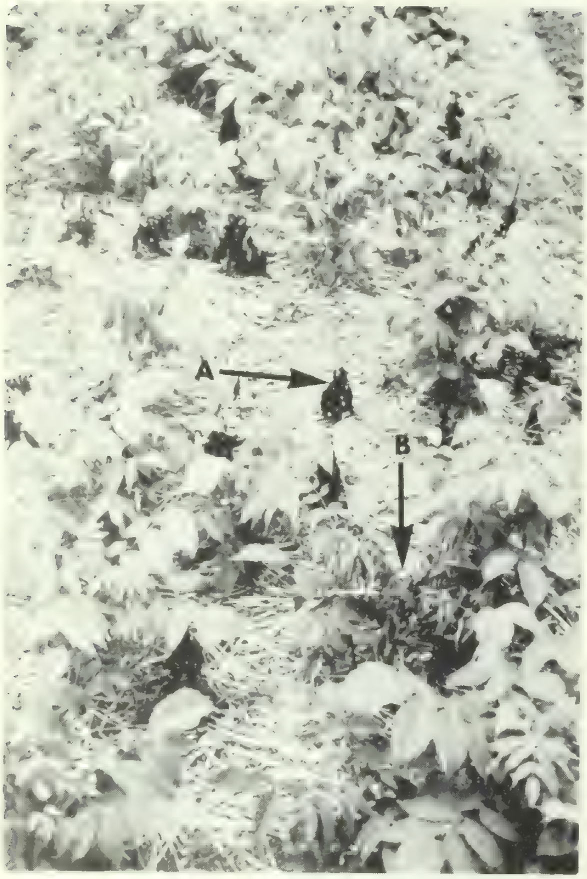

Figure 1.--Characteristic Cylindrocladium root rot symptoms of black walnut seedlings in naturally infested soil, including poor stand, dead seedlings (A) and wilting (B).

One of the most promising chemicals for the control of Cylindrocladium spp. is sodium azide (Smite 15G). Smite has effectively controlled Cylindrocladium black rot of peanuts incited by C. crotalariae, in greenhouse (10) and field (18, 20) tests at rates from 33 to 120 kg/ha. Weaver (26) obtained 100% control of Cylindrocladium root rot of peaches, incited by C. floridanum, in greenhouse tests with potassium azide at 20 mg/kg soil.

METHODS AND MATERIALS

In the fall of 1975 and 1976, fumigation test plots for the control of Cylindrocladium root rot of black walnut were established at the Griffith State Forest Nursery, Clayton, NC. Each plot was 10.4 x 1.8 m. A 0.61 m buffer zone at each end of the plot was not treated; therefore, the total fumigated area was 9.1 x 1.8 m. Five treatments, each replicated four times, were randomly distributed among the 20 test plots in a split-plot design. The efficacy of Smite (Sodium azide, PPG Industries, Inc., Pittsburgh, PA) granules (15% a.i.) and MC-33 at different rates and application methods were evaluated. The soil type of the upper profile was a loamy sand (sand = 83.6%; silt = 12.4% clay = 4.2%) although a high-clay subsoil horizon (45%) at varying depths was present.

Smite was applied by the plow-down method developed by Aaron Womble of PPG (unpublished). One-half of the Smite was applied with a Gandy gravity-flow granular applicator, and then thoroughly disked into the upper 15 cm of soil. The plot was then deep plowed, inverting the upper layer containing the Smite. The second half of the Smite was applied and thoroughly disked into the upper 15 cm of soil. This procedure effectively distributed the Smite throughout the top of 20-30 cm of soil, depending on the depth of the plow layer. The MC-33 was applied by standard soil injection to a depth of 12-20 cm, following plow-down treatment of the plow layer. The soil temperature (15-cm depth) for the 1975 and 1976 treatments were 17 C and 10 C, respectively.

The 1975 treatments, made on October 23, were as follows: Smite at 67 kg ai/ha, Smite at 224 kg ai/ha, MC-33 at 504 kg ai/ha and two non-fumigated, but plow-down-worked, controls. All plots were tarped with 1-mil polyethylene.

The 1976 treatments, made on November 4, were modified based on 1975 results. The treatments were as follows: non-fumigated control; MC-33 at 542 kg ai/ha; Smite at 224 kg ai/ha, tarped; Smite at 224 kg ai/ha, no tarp; and Smite at 224 kg ai/ha, no tarp, but in this treatment a bedshaper was utilized to increase the depth of the root zone to 31-46 cm. Typically, the root zone in this nursery ranged from 22-23 cm in depth.

On March 23, 1976 and April 4, 1977, black walnut seeds were planted in the test plots. The planted seeds were mulched with approximately 2.5 cm of pine needles. On

November 4, 1976, and November 7, 1977, 10 random black walnut seedlings for each of four replications were dug up and the taproot was dissected to determine disease severity. The ratings were based on the following scale: 0 = healthy; 1 = necrosis at tip of tap root only (less than 5% of the taproot); 2 = necrosis extending slightly into root stele and cortex from root tip (less than 20% of tap root); 3 = necrosis of 20 to 50% of tap root; 4 = necrosis of more than 50% of tap root; 5 = dead.

Prior to fumigation in the fall and planting in the spring, five soil samples (0 - 10 cm depth) per plot were collected and placed in plastic bags with pinholes for gas exchange. Samples were stored at room temperature (26-28 C) until processing. The presence of Cylindrocladium inoculum in soil was determined by the azalea-leaf-trap method (15), due to the low inoculum levels present. Ten azalea leaves ('Hershey Red') were placed in each previously mixed soil sample and incubated for 5-9 d at 26-28 C in moist chambers. Following incubation, the leaves were surface-sterilized in 0.5% NaClO for 5 min, rinsed in sterile distilled water and the margins of necrotic lesions plated on sucrose-thiabendazole (TBZ) medium, selective for Cylindrocladium spp. (14).

Tissues from symptomatic walnut roots were surface sterilized for 3 min in 1.0% NaClO, rinsed in sterile distilled water and the margins of necrotic areas placed on Cylindrocladium-selective media (7, 14).

Artificial soil clods (1.3, 2.5, and 5.1 cm in length) were produced from two Cylindrocladium-free soils of different clay contents (43% and 8%), bulk densities (1.4 and 1.7) and field capacities (32% and 12% water) but equal pH values (6.2). Microsclerotia of C. crotalariae were placed at the clod center in a layer of artificially infested soil 1.2-cm thick. Smite granules (8% a.i.) were used in all experiments. Each of the soils (air dry) was thoroughly mixed with Smite at the rate of 50 μg/g soil, equivalent to approximately 112 kg ai/ha - 15 cm depth, for 30 min in a plastic bag before placing it in a plastic container (31 x 23 x 10 cm) to a depth of 4 cm, and then raising the water content of the soil to field capacity. The clods, containing no Smite, were randomly placed near, but not at the bottom of the 4-cm layer of Smite-treated soil or control soil during placement of the soils in the boxes. In addition, 20 g of microsclerotia-infested soil were spread over each of three Whatman filter papers (9-cm diam), and the papers were placed on top of the treated or control soils (to simulate microsclerotia in surface debris) in the containers. For soils receiving a surface treatment of Smite (10 μg ai/g soil), granules of the latter were spread evenly over the soil surface not covered by the three filter papers. Thus, no direct contact was made between the Smite and microsclerotia-infested soil. The containers with treated or control soils were covered with loose-fitting plastic lids. After 4d of incubation at 27C all microsclerotia-infested soils were assaved for C. crotalariae microsclerotium populations by the Krigsvold and Griffin method (14).

Field studies of Cylindrocladium populations at the Augusta Forestry Center, Crimora, VA were undertaken during the summer of 1975, 1976 and 1977. Soil samples (0-20 cm depth) were collected from black walnut seedbeds and assayed qualitatively by the azalea-leaf-trap method (15) and quantitatively by wet sieving and dilution plating (14). Cylindrocladium populations in rotted black walnut roots were determined by a modification of the Krigsvold and Griffin method (14) for Cylindrocladium soil population analysis. Severely rotted black walnut roots (50-g samples) were ground up in a Waring Blender for 5 min at high speed, followed by wet-sieving through 841-um (20 mesh) and 44-um sieve and washed into a beaker with 250 ml of sterile distilled water. The suspension was stirred for 30 sec with 10 ml of 5% NaClO and rinsed through a 44-um sieve for an additional 3 min. Dilutions of 1:25 (root tissue:sterile distilled water) were used and 1 ml was pipetted onto each of 10 petri dishes containing sucrose-TBZ selective medium (14). Cylindrocladium populations were determined from counting colonies developing on each of 10 petri dishes after 7 d incubation.

Tissue from margins of necrotic roots was surface sterilized for 3 min in 1.0% NaClO and rinsed in sterile distilled water prior to plating. Feeder roots were rinsed under running tap water for 30 min and plated on media selective for Cylindrocladium (7, 14).

To survey the Augusta Nursery for Cylindrocladium inoculum, soil samples were taken throughout the nursery at 15-m intervals along approximately 150-m rows (approximately 75 m apart) during June and August 1977. The presence of Cylindrocladium spp. was determined by the azalea-leaf-trap method (15) previously described.

For pathogenicity tests, black walnut seeds were grown in a potting mixture containing 1 part vermiculite, 1 part weblite (an expanded shale product, Weblite Corp., Roanoke, VA 24029), and 0.5 part peat moss. For inoculum, clones of *C. floridanum*, *C. scoparium* and *C. parvum* isolated directly from necrotic black walnut roots were grown in a liquid medium (12) for 6-9 mon at 25 C in continuous darkness. In 1976, seedlings were transplanted into 26.7-cm diam. pots containing potting mix artificially infested with 10 *C. floridanum* microsclerotia/g mix or 150 ml of *C. parvum* mycelium-chlamydospore preparation per pot. The latter was prepared by washing the *C. parvum* mycelium-chlamydospore mat for 10 min in tapwater, followed by grinding the washed mat in a Waring Blender for 5 min. In 1977 and 1978 seedlings were transplanted into 12 cm (diam) plastic pots and placed in controlled temperature (25 C) tanks. In 1978, seedlings were grown under continuous light. Tap roots of eight-week-old black walnut seedlings were wounded (approximately 1.5 cm of the root surface was peeled off) and inoculated with a washed mat (15 mg portions, dry weight) of *C. scoparium* and *C. parvum* alone or in combination. Wounded, uninoculated plants served as controls. Each treatment was replicated ten times in 1977 and twenty times in 1978. Seedlings were harvested after five weeks incubation, and rated according to the disease severity index previously described. Pathogen isolation from margins of necrotic roots was done as described above.

RESULTS

Control of Cylindrocladium Root Rot

Root disease severity ratings from the 1975-76 test indicated that more healthy seedlings (disease class 0) were obtained from plots fumigated with 224 kg ai/ha Smite than with other treatments (table 1). However, when the probable effect of root pruning or undercutting is considered (combined disease classes 0 and 1) control of root rot with MC-33 (405 kg ai/ha) and Smite (224 kg ai/ha) may be comparable. Root disease index ratings for Smite (224 kg ai/ha) were significantly lower than both controls, but were not significantly different from the MC-33 treatment ($\underline{P} = 0.05$). Smite at 67 kg ai/ha was only marginally effective in disease control. Azalea-leaf-trap assays of soil samples collected from treatment plots indicated that the soil fumigations generally resulted in inoculum decreases.

The 1976-77 chemical treatments were modified and the plot location was moved to area believed to contain higher levels of *Cylindrocladium* inoculum than in the 1976-77 plots (C. E. Cordell, personal communication However, azalea-leaf-trap assays indicated t inoculum levels were comparable to the 1975- levels (mean isolation percentage from traps of soil samples prior to fumigation = 9%). Compared to the 1975-76 severity ratings, disease ratings were low throughout the plot The mean percent of living plants in all tre ments in disease severity classes 0 and 1 wa 87%. No treatments were significantly diffe from the control ($\underline{P} = 0.05$). Further, measu ments of lengths of healthy seedling tap roo in each treatment were not appreciably diffe However, chemical treatments reduced the *Cylindrocladium* inoculum level, based on azalea-leaf-trap assays. In both years, *C. floridanum* was recovered from margins of symptomatic black walnut roots. Percentage successful isolation of *C. floridanum* from necrotic roots was approximately 25%.

In most cases, root rot of seedlings wa evident at the tip of the tap root for both control and chemical-treatment plots, and colonization appeared to progress up the vas- lar system for many plants (fig. 2). Initia necrotic symptoms were sometimes evident at the root crown. In some instances, taproot elongation was restricted by the presence of high-clay subsoil (45% clay) located close t the soil surface. Observations indicated th much of the root rot was associated with thi high-clay soil or the interface of the plow layer and the high-clay soil (fig. 3).

Separate experiments indicated that fumigation of low-clay soil clods (1.3 to 5.1 c in length) with Smite resulted in a complete kill of artificially infested microsclerotia In contrast, all microsclerotia in fumigated high-clay soil clods of 5.1 cm in length wer not killed, (32% of the microsclerotia survi although no microsclerotia were recovered fr fumigated clods of 1.3 and 2.5 cm in length. When a surface treatment of Smite was made i addition to the standard Smite soil-mix, microsclerotia in large (5.1 cm) high-clay clods were killed.

Biology of Cylindrocladium spp. at the Augusta Forestry Center, Crimora, VA

A small spored specie of *Cylindrocladiu* resembling *C. parvum*, was consistently recov from diseased black walnut roots and from so at the Augusta Forestry Center. Conidia wer one septate and ranged in size from 9.5 - 21 x 2.1 - 4.3 μm (mean = 15.5 x 3.0 μm).

Table 1. Effect of Smite and MC-33 chemical treatments on Cylindrocladium root rot development of black walnut seedlings at the Griffith State Forestry Nursery, Clayton, NC, in 1975-1976.

Treatment[a]		Rate - kg (ai/ha)	Percent of live plants in disease severity class[b]				Percent Dead plants[c]	
			0	1	2	3	4	5
MC-33	yz	504	52.5	32.5	10.0	5.0		
Smite	y	34 + 34 plow-down method	40.0	22.5	37.5			
Smite	z	112 + 112 plow-down method	70.0	12.5	17.5			
Control I	xy		32.5	37.5	22.5	5.0	2.5	3.0
Control II	x		22.5	35.0	20.0	12.5	5.0	13.0

[a] MC-33 = methyl bromide 66%, chloropicrin 33%, Smite = sodium azide, 15% granule. Treatments followed by the same letter are not significantly different (P = 0.05) according to Duncan's multiple range test. Control I and Control II were identical entries.

[b] Class values determined by dissections of seedling taproot.

Percent of 40 random black walnut seedlings, 10 seedlings per replication for each of four replications.

0 = healthy; 1 = necrosis at tip of taproot only (less than 5% of the taproot); 2 = necrosis extending slightly into root stele and cortex from root tip (less than 20% of taproot); 3 = necrosis of less than 50% of taproot; 4 = necrosis of more than 50% of taproot; 5 = dead.

[c] Percent of total seedlings, ave. 40 seedlings per replication, 4 replications per treatment.

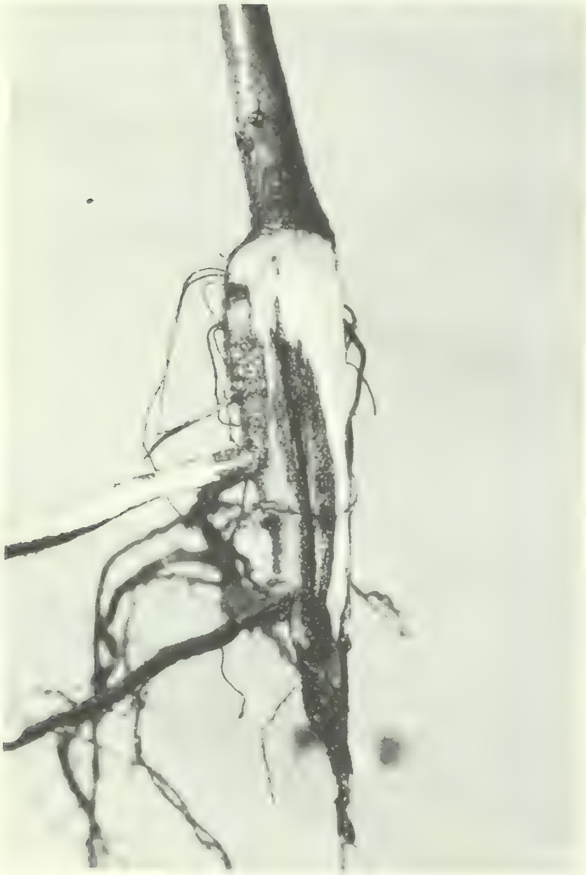

Figure 2. Cylindrocladium root rot of black walnut seedlings.

Figure 3. Association of root rot of black walnut seedlings (arrow) with high-clay so

Vesicles were abundant but extremely variable in morphology (clavate to papillate) and size [11.9 - 59.5 x 2.4 - 14.3 µm (mean = 26.8 x 6.6 µm)]. Unlike *C. crotalariae*, *C. floridanum* and *C. scoparium* which produce microsclerotia, this fungus produces chlamydospore-like structures. This species will be referred to as *C. parvum* in the following sections.

Isolations from azalea-leaf-trap assays of soil samples collected from the rooting zone of necrotic black walnut seedlings and soil dilution plating indicated that the population of *Cylindrocladium* spp. was generally low at the Augusta nursery. *Cylindrocladium parvum* was isolated from azalea-leaf-traps of soil more frequently than *C. scoparium* and *C. floridanum* (mean of 9 soil samples = 34% for *C. parvum* and 3% for *C. scoparium* and *C. floridanum*). Quantitative population assays in 1976 by the soil-dilution method (14) yielded a mean of 9.9 propagules/g soil (range = 3-17. propagules/g soil) of *C. parvum* for three seedbed soils containing many dead black walnut seedlings. The mean population of *C. scoparium* was 1.0 propagule/g (range = 0 - propagules/g soil), whereas *C. floridanum* was recovered only infrequently. Populations in soil samples collected from the 1975 black walnut seedbeds were lower. The mean population of *C. parvum*, *C. floridanum*, and *C. scoparium* from six soils collected from root zones of severely necrotic seedlings was 5 (range 2 - 13), 0 and 0 propagules/g soil, respectivel by the soil-dilution method. No *Cylindrocladi* spp. were recovered in two trials using the Thies and Patton procedure (23) or the alfalf leaf bioassay method (3). Extremely high populations of *C. parvum* (mean = 1,107 propagules/g root) were found from five samples of dead seedling roots. Populations of *C. floridanum* and *C. scoparium* in severely necrotic roots were lower (mean = 385 propagules/g roo than for *C. parvum*.

Typically, a low percentage successful isolation of Cylindrocladium spp. from marginal necrotic tissue of seedlings with characteristic root rot symptoms was found using sucrose-TBZ medium (14). For C. parvum and C. scoparium, percentage isolation from 485 seedlings was 27.7% and 11.0%, respectively. Cylindrocladium floridanum was isolated infrequently. No Cylindrocladium spp. were recovered when tissues were plated on semi-selective media including acidified potato-dextrose and acidified Czapek-Dox agar (Difco).

Disease incidence and severity was high in the 1976 black walnut seedbeds, approaching high values in localized "hot spots" (55% of the bed area had an average of 40% seeding kill). In seedbeds of this block, root rot appeared to progress outward from centers as the season progressed. The incidence of root rot was appreciably lower (ca. 5%) in 1975.

A nursery-wide survey of seedbed soils indicated that Cylindrocladium spp. are widely distributed but that inoculum density (estimated from percent colonization of azalea-leaf-traps) is low. In a block never planted in black walnuts, no recovery of any Cylindrocladium spp. was found; however, the highest percentage recovery (22%) was found from soil samples collected from the site of the 1976 black walnut seedbeds. Recovery of Cylindrocladium spp. in the four other blocks in the nursery ranged from 6 to 11% (mean = 9%).

A low percentage root rot was found for black walnut seedlings inoculated with C. scoparium and C. parvum in 1976. No seedlings in potting mix artificially infested with C. parvum or C. parvum and C. floridanum developed root rot. Twenty percent (2/10) of seedlings grown in C. floridanum-infested mix developed root rot symptoms; however, necrosis was not evident in the root stele. The low percentage symptoms observed was probably due to excessively high greenhouse temperatures (maximum = 42.2 C). Soil temperatures above 30 C are unfavorable for Cylindrocladium root rot development of peach (27) and peanut (19).

In 1977, no control seedlings developed root rot but 20% and 30% of the C.parvum- and C. scoparium- inoculated seedlings, respectively, developed root rot. Cylindrocladium parvum and C. scoparium were isolated from margins of necrotic tissue.

In 1978, approximately one week after inoculation, one seedling inoculated with C. scoparium began to wilt and after two weeks, severe root rot symptoms, characteristic of Cylindrocladium root rot, were observed. Percentage incidence of root rot in seedlings inoculated with C. parvum, C. scoparium, and C. parvum plus C. scoparium was 15, 20, and 10%, respectively. Necrosis was observed in the root stele of 10% and 5%, respectively, of the seedlings in the C. scoparium and C. parvum treatments. Isolations from symptomatic roots yielded C. scoparium and C. parvum.

DISCUSSION

Chemical control tests, undertaken from 1975 to 1977, were complicated by the low level of root disease present. This is surprising because Cordell (4), in 1971, estimated that at least 70% of 75,000 1-0 black walnut seedlings had symptoms of Cylindrocladium root rot. In 1973, he repeatedly isolated C. scoparium from soil samples collected from the site of the 1971 epiphytotic. The test plots in the present study were located in the vicinity of the 1971 epiphytotic. The decreased disease observed in 1976-77, compared to 1975-76 must be due in part, to environmental conditions since differences in Cylindrocladium inoculum for both years was not apparent. An unusually dry summer in 1977 may have been a contributing factor in the low amount of root rot observed in the 1976-77 tests.

Control of Cylindrocladium root rot of black walnut seedlings is complicated by several factors. Cylindrocladium microsclerotia are capable of long-term survival (16, 17, 23) and successful infection can develop at low inoculum densities (9, 10). Thus, nearly complete kill of microsclerotia may be necessary for adequate control. Further, black walnut is a deep-rooted species and deep placement of fumigants is required to provide protection for the entire root system.

A high-clay horizon (18-28 cm below the soil surface), was observed in the treatment plots and was associated with root rot development in many instances. Decreased hydrazoic acid diffusion and thus penetration, as a result of low-percentage large-pore spaces, may reduce fumigant efficiency in high-clay soils. During seedbed preparation, clay clods with the smallest dimensions as large as 6.3 cm (mean size = 4.3 cm) were brought to the soil surface in some areas of the seedbed, and root rot was associated with this high-clay soil. To obtain maximum disease control seedbed soil must be disked or rototilled to eliminate all large soil clods. At the Griffith nursery, the depth of the plot layer was limited by the clay horizon close to the soil surface, and pockets of sandy-loam soil were observed below the plow layer. Thus, complete mixing of chemicals by plowing and disking with soil was not accomplished. The highest incidence of root rot, as previously mentioned, occurred at the tip of the seedling tap root. This was probably due, in part, to the presence of viable Cylindrocladium microsclerotia in undisturbed sandy-loam soil pockets below the plow layer and at the interface of the plow layer and the high-clay soil.

The plow-down method offers a simple and efficient method to incorporate granular chemicals deep and widely distributed in the rooting zone. However, all Cylindrocladium microsclerotia were not killed by soil fumigation with high rates of Smite, as indicated by azalea-leaf-trap assays and root rot development. Thus, it appears that alternate control practices are necessary in combination with fumigation. Effective grading of seedlings together with root pruning and fungicide dips may offer such an alternative. Cordell (4) found that seedlings with more than 10% root rot and a stem base less than 9.5 diameter had a poor chance of outplanting survival. Similarly, grading black walnut seedlings based on lengths of healthy taproot may give a satisfactory estimate of outplanting seedling survival.

Previously, C. parvum has been associated with root rot of rose, grape and Telopea speciossima, but pathogenicity has not been demonstrated (1, 2). Cylindrocladium parvum is either a causal factor in the black walnut root disease or is a proficient secondary colonizer. The presence of C. parvum in the margins of necrotic roots and the extremely high populations in severely necrotic roots, argues against the latter. Greenhouse tests deomonstrated only limited pathogenicity by C. parvum, but similar results were obtained also with a known pathogen (C. scoparium). The Cylindrocladium isolates utilized in the present studies were obtained from active infections, transferred one to two times and stored under mineral oil. Thus, they should have been pathogenic. Possibly, resistance to Cylindrocladium root rot is quantitative and dependent upon host vigor and environmental conditions (19). The black walnut seedlings in the 1977 and 1978 pathogenicity tests were very vigorous, and provided with optimum levels of water, fertilizer and light. Further work is required to elucidate the role of physical and biotic environmental factors in Cylindrocladium root rot development of black walnut seedlings.

Distribution of Cylindrocladium spp. throughout the Augusta nursery appears to be dependent, in part, upon the black walnut cropping history of each location. For instance, no walnuts were ever grown and no Cylindrocladium spp. were isolated from soil samples collected from one block of nursery. Disease incidence and severity was appreciably higher in 1976 than in 1975, and the percentage recovery of Cylindrocladium spp. was greater from the block where the 1976 black walnuts were planted than from the 1975 block. Possibl a greater number of microsclerotia were released into the soil upon decomposition of necrotic black walnut roots. At the survey sampling time (July), disease incidence and severity in the 1977 black walnut crop were low. Few soil samples from this block in the survey were positive for Cylindrocladium.

Soil air-drying and low soil temperatures (<6C) results in large decreases in germinability of Cylindrocladium microsclerotia (6, 8, 21, 24); however, partial reversal of the decreased germinability occur upon rewetting air-dried soils and incubation at 25 C of low-temperature-treated soils (8, 21). Impairment of microsclerotium germinability following exposure to drought or low soil temperature may affect survival, or delay and reduce disease development, even though a complete loss of viability does not occur.

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GROUP DISCUSSION

Green: You showed what appeared to be a mulch on the seedbed. Is that routine practice?

Roth: In this nursery they mulch with straw and in North Carolina they mulch with pine needles about 2-3 inches deep.

Green: Do you find *Cylindrocladium* associated with areas of poor soil drainage?

Roth: No. For example, much of our problem occurred right in the middle of the seedbeds which were raised a little bit higher than the poorer drained ends of the beds.

Green: In Indiana nurseries where the hydromulch was used the incidence of *Phytophthora* root rot was much higher because of the increased soil moisture retained at the surface.

Kuntz: In Wisconsin we have a somewhat different situation. *Cylindrocladium* levels are low in the seedbeds. Our real problems develop in the heeling-in beds. In the spring following heeling-in we come out with almost total losses of heeled-in bundles. Where do you think these infections come from? Are they latent infections that develop in a more favorable environment in the heeling-in beds or is it infection that occurs as a result of wounding during the lifting/heeling-in sequence?

Roth: In the Southeast they are not heeled-in--they are put in cold storage in bundles. The seedlings that have root rot when they are put into cold storage have a poor outplanting survival rate and those that appear healthy going into cold storage have a high survival rate. Wounding may also be a factor. In greenhouse inoculation tests when I wounded the plants I got a much higher infection rate.

Kuntz: If we leave the seedlings in the seedbed until spring and then lift them we avoid practically all of this problem. Nurserymen maintain, however, that they can't do all of this work in the spring and they've got to be lifted in the fall.

Nicholls: At the Wilson State Nursery in Wisconsin a loss of around 90 percent occurred in a bed of 200,000 walnut seedlings that were planted in an unfumigated bed. In this instance no root pruning or lifting injuries were present that could be related to the development of the root rot.

Shigo: Years ago, I worked on a similar crown and root rot problem of yellow birch and found that where many plants occurred in small areas of nursery beds there often was a salts accumulation problem in the upper soil levels. Have you ever considered this phenomenon as one of the factors involved in the root rot problem?

Roth: With *Cylindrocladium*, at least in this one nursery, with a high clay content, most of the infection was of the lower tap root. In other nurseries with soils with less cla the rot really wasn't limited eith to the crown or lower tap root--it came in from lateral roots or root at any location.

Shigo: But I am talking about the more or less severe alterations in salt concentrations that occur in the top 4-6 inches of soil.

Roth: With black walnut, the tap root ge a lot deeper than that and infecti are seen down through 25 cm.

Green: You're thinking about root necrosi as a result of high salt concentra tions?

Shigo: Salt as a contribution factor. Something's got to be weakened som how, and I'm just wondering if thi factor was one you've considered. You need to determine in your layering effect if you had such a situation.

LaMadeline: Is there a relationship between *Phytophthora* and *Cylindrocladium* root rots to fertilization--especially nitrogen?

Roth: We didn't test this in the field. In the greenhouse those factors of light, moisture and nutrition which led to optimal walnut growth seemed to result in increased resistance to *Cylindrocladium* infections.

THE WALNUT CATERPILLAR, DATANA INTEGERRIMA G. & R.

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ABSTRACT.--A description of the adult, egg, and larval stadia of the walnut caterpillar, Datana integerrima, is given. In central Illinois there is 1 generation of the walnut caterpillar a year, but occassionally 2 generations occur during certain years. There are 2 generations a year in southern Illinois. First generation adults emerge in mid to late May in southern Illinois; 2nd generation adults emerge in late July. Larval feeding habits vary in the 1st, 2nd, and 3rd stadia. Larvae of the walnut caterpillar feed and survive only on species of Juglandaceae. Four species of Tachinidae: Diptera and 4 species of Ichneumonidae: Hymenoptera parasitize larvae of the walnut caterpillar; 5 insect predators and 2 spiders were captured while feeding on walnut caterpillar larvae; and the house mouse and white footed mouse feed on walnut caterpillar pupae. Foliar sprays of malathion, diazinon, acepthate, and Bacillus thuringiensis Berliner controlled 2nd and 4th instar larvae.

The walnut caterpillar, Datana integerrima, is an important defoliating pest of black walnut, Juglans nigra L. Such defoliation weakens trees and can lead to invasion by secondary insects (Kulman 1971). Defoliation also affects development of the nut. The kernal does not develop fully after a tree has been defoliated (Hixson 1941).

The insect occurs throughout eastern United States and in some areas of southern Canada (Baker 1972). The insects range extends as far west as Minnesota, Nebraska, Kansas, Oklahoma, and as far south as Pecos and Terrell Counties in southwest Texas (Hixson 1941, Neeb 1976).

The adult of the walnut caterpillar varies in size according to sex; the body length of the male (Figure 1) is ca. 2 cm and the female is ca. 2.3 cm in length. The scales of the head and upper thorax are a deep rust-brown and are displayed prominently above the wings when in a resting position. The forewing is dark beige with 4 bands of dark rust-brown traversing it from the anterior to the posterior wing margin; a 5th band is present, but it is usually conterminous with the 4th. The hindwing, lowe thorax, and abdomen are pale beige. The upper abdomen is a rust color, but is much lighter than the upper thorax.

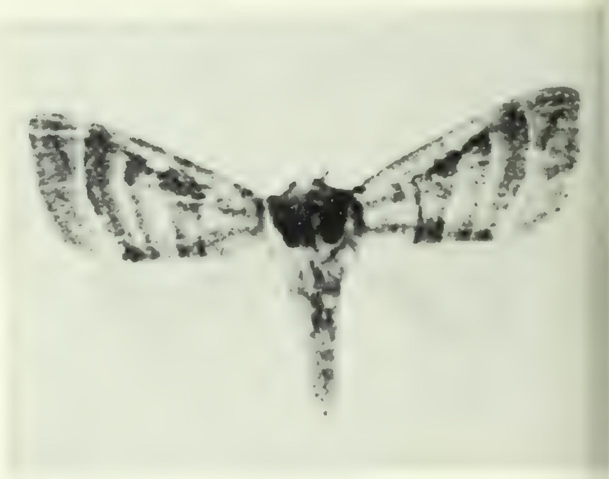


Figure 1.--An adult male of the walnut caterpillar, Datana integerrima.

The egg of the walnut caterpillar (Figure 2) is ca. 0.5 mm in diameter and 0.7 mm in height. The egg initially is very pale green with a white cap. Later the green disappears and becomes a very pale blue-green. The white cap does not change color. The eggs are cement to the lower surface of the leaflet and are placed in masses with slightly curving rows. There is an average of 621 eggs in each mass.

The 1st instar larva is light green with a black head capsule (Figure 3). Several long white setae arise from black tubercles along the dorsal and lateral areas of the body. Ther is a black prothoracic and anal shield. Late 1st instar larvae show some red in the thoracic and lateral abdominal areas, and faint dorsal and lateral lines. The 2nd, 3rd, and 4th insta larvae are red-brown with black head capsules, white setae, and white dorsal and lateral lines the length of the body. The 5th instar larva is black with a black head capsule, white setae and white dorsal and lateral lines; however, the lines are not as evident as in earlier instars (Figure 4). The 2nd, 3rd, and 4th instars have a black prothoracic and anal shield. The shields are present in the 5th instar, but are the same color as the larval body and are not easily seen.

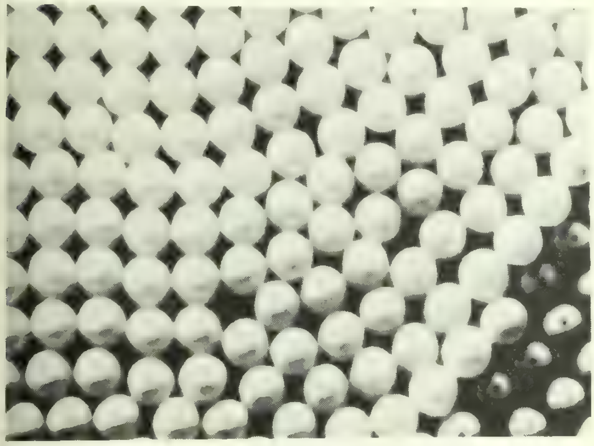


Figure 2.--Eggs of the walnut caterpillar, Datana integerrima, on the lower surface of a black walnut leaflet.

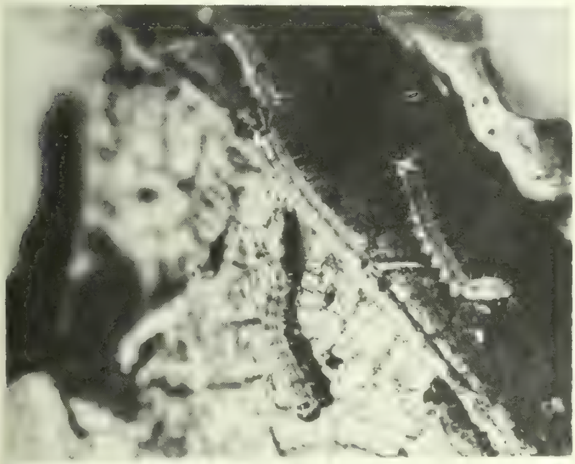


Figure 3.--1st instar larvae of the walnut caterpillar, Datana integerrima, on black walnut foliage.

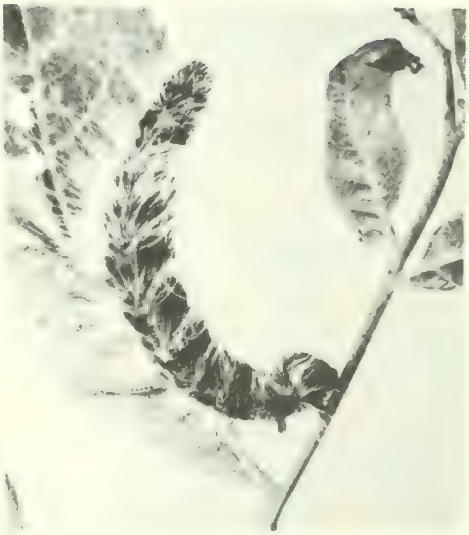


Figure 4.--A 5th instar larva of the walnut caterpillar, Datana integerrima, on black walnut foliage.

The approximate body lengths of the various instars are as follows: 1st instar 2 mm to 4 mm; 2nd instar 4 mm to 9 mm; 3rd instar 9 mm to 14 mm; 4th instar 14 mm to 27 mm; and 5th instar 27 mm to 47 mm at maturity.

There are 2 generations of walnut caterpillar a year in southern Illinois, 1 generation in central Illinois with a potential 2nd generation. First generation adults begin emerging from overwintering pupae in mid May reaching a peak emergence in late May in southern Illinois. Second generation adults emerge in mid July reaching a peak in late July.

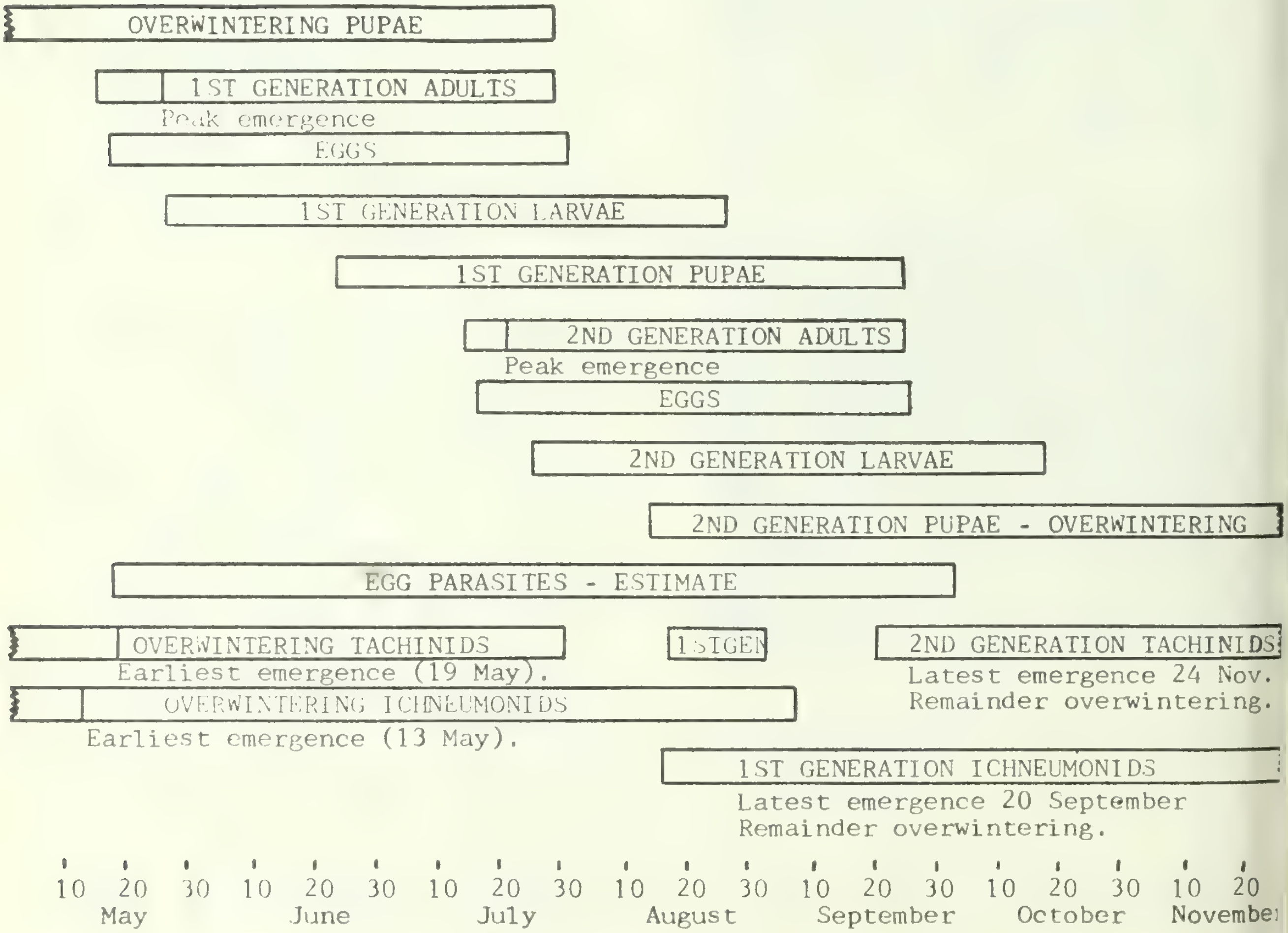
The adults oviposit in ca. 2 days after emergence. Egg masses are found on the lower surface of the leaflets and are generally on the lower branches of the host plant that is growing along the margins or in openings of hardwood forests, or on open grown trees such as ornamentals or those in plantings.

Larval eclosion occurs in ca. 9 days after egg deposition. The larvae mature in an average of 27 days; however, in very warm weather with temperatures averaging 25.2 degrees C the larval duration is shortened to ca. 19 days. Most 2nd generation larvae mature and drop from the trees to pupate in the soil by late September. The larvae require ca. 2 days to pupate, form no cocoon, and most pupate from 1 to 2 cm deep in sod.

The seasonal history of the walnut caterpillar and it's parasites is shown in table 1.

Host plants include black walnut, Juglans nigra L., butternut, J. cinerea L., various species of hickory and pecan, Carya sp., and, where planted in the insects range, English or Circassian walnut, J. regia L. The walnut caterpillar has been reported on various other tree and shrub species, but food preference tests indicate that the larvae of the insect feed and survive only on species of the Juglandaceae.

Table 1.--Seasonal history of the walnut caterpillar and its parasites in Pope County, Illinois. Based on median emergence dates determined from weather records for a 5-year period 1973 through 1977 in Pope County, Illinois.



Plants used in food preference experiments are shown in table 2.

Table 2.--Plant species used to determine if walnut caterpillar larvae will feed on any plant other than species of Juglandaceae

Common name	Plant species
Apple	Malus sp.
Azalea	Rhododendron sp.
Blackgum	Nyssa sylvatica Marsh.
Black locust	Robinia pseudoacacia L.
Hawthorn	Crataegus sp.
Hazlenut	Corylus americana Walt.
Honey locust	Gleditsia triacanthos L.
Multiflora rose	Rosa multiflora Thunb.
Redbud	Cercis canadensis L.
Red oak	Quercus shumardii Thunb.
Shingle oak	Quercus imbricaria Michx.
White oak	Quercus alba L.
Post oak	Quercus stellata Wang.
Sassafrass	Sassafrass albidum (Nutt.)
Southern catalpa	Catalpa bignonioides Walt.
Sugar maple	Acer saccharum Marsh.
Winged elm	Ulmus alata Michx.
Black willow	Salix nigra Marsh.
Persimmon	Diospyros virginiana L.

Unfed and fed 1st and early 3rd instar larvae did feed on persimmon, but did not survive. Black walnut and shagbark hickory, Carya ovata (Mill.), were used as check plants. In tests to determine food preferences between black walnut and shagbark hickory, the larvae selected the hickory sp. over black walnut at a statistically significant level greater than 0.05%.

Some confusion may occur in food preferences because the walnut caterpillar larvae abandon a tree when the foliage becomes sparse or when it has been defoliated. The larvae will scatter in all directions upon leaving the tree and are apt to ascend any nearby plant. Larvae abandoning defoliated black walnut trees were found on goldenrod, Solidago sp., horseweed, Erigeron canadensis (L.), daisy fleabane, Erigeron annuus (L.), blackberry, Rubus sp., sugar maple, Acer saccharum Marsh., shingle oak, Quercus imbricaria Michx., winged elm, Ulmus alata Michx., and various grasses in the area. Other larvae that had abandoned defoliated black walnut trees were found on sycamore, Platanus occidentalis L., tuliptree, Liriodendron tulipifera L., sweetgum, Liquidambar styraciflua L., and Scotch pine, Pinus sylvestris L. Little or no feeding occurred on any of the trees, weeds, or grasses on which the larvae were found. All but 1 larva had abandoned the plants listed above within 24 hours.

Larval feeding habits vary with the instar. Upon eclosion 1st instar larvae move to the upper surface of the leaflet on which the egg mass is located and devour the surface tissues giving the leaflet a skeletonized appearance. After feeding on the upper leaflet surface the larvae expand their feeding activities to nearby leaflets, and then feed on either surface. The amount of feeding by 1st instar larvae on the lower surface of the leaflet after initially feeding on the upper surface is probably dependent upon the pubescence of the leaflet.

Second instar larvae feed from the edge of the leaflet and devour the entire leaflet except the larger veins. Later they leave only the main vein. Third instar larvae leave the main vein at first, but later leave only a petiolar stub as do the 4th and 5th instars.

Four Tachinidae and 4 Ichneumonidae parasitize the walnut caterpillar larvae. The parasites and the walnut caterpillar life stage from which they were recovered are shown in table 3.

Insects found feeding on walnut caterpillar larvae were identified as the hemipterans Podisus maculiventris (Say)[1], Arilus cristatus (L.)[2], the hymenopteran Vespula maculifrons (Buysson)[3], and unidentified species of Diptera (Asilidae), and unidentified nymphal Orthoptera (Tettigoniidae). Two immature spiders identified as Misumenops sp. and Phiddipus sp.[4] were also found feeding on walnut caterpillar larvae.

Vertebrate predators of walnut caterpillar pupae include the house mouse, Mus musculus L.[5], and the white-footed mouse, Peromyscus leucopus[5]. The caterpillar pupae offered these mice were eaten before corn and soybeans given to the mice at the same time.

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[1] Determined by J. McPherson, Southern Illinois University, Carbondale, Illinois.

[2] Determined by D. W. Webb, Faunistics Section, Illinois Natural History Survey, Urbana, Illinois.

[3] Determined by W. E. LaBerge, Faunistics Section, Illinois Natural History Survey, Urbana, Illinois.

[4] Determined by J. E. Unzinger, Faunistics Section, Illinois Natural History Survey, Urbana, Illinois.

[5] Determined by S. P. Havera, Wildlife Research Section, Illinois Natural History Survey, Urbana, Illinois.

Table 3.--Tachinid and ichneumonid parasites emerging from walnut caterpillar cultures in Pope and Champaign Counties, Illinois

Name	Family	Walnut caterpillar stage
Archytas metallicus (R.D.)[1]	Tachinidae	Emerge from caterpillar pupa.
Belbosia semiflava Aldrich[1]	"	"
Lespesia datanarum (Townsend)[1]	"	"
Unidentified		Tachinid larva emerge from caterpillar larva.
Bathylypa paeneferruginea (Vier.)[2]	Ichneumonidae	Emerge from caterpillar pupa.
Tamypelma datanae (Riley)[2]	"	"
Tamypelma fulvicorne (Twns.)[2]	"	"
Unidentified		Emerge from 4th instar caterpillar larva.

[1] Determined by C. W. Sabrosky, U.S.D.A. Systematic Entomology Laboratory, Beltsville, Maryland.

[2] Determined by W. E. LaBerge, Faunistics Section, Illinois Natural History Survey, Urbana, Illinois.

The yellow-billed cuckoo, *Coceyzus americana*, was observed frequenting infested black walnut trees growing in a bushy area on the margin of a forest. It cannot be verified that the bird fed upon the walnut caterpillar larvae; however, this bird species is a known predator of other hairy caterpillar species.

A microsporidian, *Nosema necatrix* Kramer[6], was found to be at lethal levels in tissues of 14 out of 20 dead 5th instar larvae. Three of the 6 remaining larvae were dead from bacterial septasemia[6]; the remaining 3 had no pathogenic agent in the tissues. An unidentified virus[6] that causes mummification of the pre-pupal larva and a bacterial agent[6] causing cuticular weakness in pupae were also found.

Predators account for ca. 49% of the larval mortality in a colony of walnut caterpillar while the microsporidian, *N. necatrix*, accounts for less than 2%. The virus causing mummification of the pre-pupal 5th instar larva accounts for ca. 56% of the mortality in the walnut caterpillar larvae reaching that stage. Pupa diseases account for approximately 60% of the mortality occurring in the pupal stage.

Over a 2 year period tachinids and ichneumonids parasitized ca. 16% of the larvae that survived predation (630 parasites were recovered from 3,938 larvae/pupae).

Chalcid[7] egg parasites emerged from ca. 21% of the eggs collected during a 2 year peri (a total of 25,084 eggs were collected). Appr mately 18% of these eggs were infertile. The chalcid egg parasite probably is more effectiv than is indicated in this study. Many of the eggs that were counted as infertile were proba parasitized, but no adult chalcids emerged fro such eggs. The eggs were black and did not dr up or cave-in as unfertilized lepidopterous eggs normally do. Some of the eggs were cut open and dead parasites were found.

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[6] Determined by J. Maddox, Section of Economic Entomology, Illinois Natural History Survey, Urbana, Illinois.

[7] Determined by W. E. LaBerge, Faunistics Section, Illinois Natural History Survey, Urba Illinois.

An estimated 15% of the walnut caterpillar pupae are eaten by the house and white-footed mouse. The white-footed mouse could be a very important control factor under natural conditions, particularly when walnut caterpillar populations are at epidemic levels. The white-footed mouse is found along the margins of hardwood forests and most naturally occurring black walnut is found in the same areas.

Foliar sprays of malathion 50EC, diazinon 25EC, acephate 75SP, and Bacillus thuringiensis Berliner were applied to 2nd and 4th instar walnut caterpillar larvae. All 4 insecticides were effective; however, at present acephate is the only insecticide of this group approved by USEPA for use on black walnut for walnut caterpillar control. None of the insecticide treatments produced evidence of phytotoxicity on black walnut.

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GROUP DISCUSSION

Weber: Given the high rate of natural control you are getting from parasites and predators, do you think it is really necessary to spray for the walnut caterpillar?

Farris: In the first generation, no; because total number of caterpillars is very low. Around Dixon Springs the second generation begins quite high in numbers. High mortality of larvae has a tendency to prevent foliage damage to the trees, but the highest percentage of mortality does not occur until after the larvae are older. Given 30 large colonies, for example, with 800-900 larvae/colony and a 50 percent mortality rate, 450 surviving larvae on 15-foot tall black walnut trees can hurt those trees. Therefore, it is still sometimes necessary to spray.

Funk: How far do the larvae migrate? When they finish off one tree and are looking for the next one, how far will they move?

Farris: I ran some tests on this. Fourth instar larvae can survive from 176 to 196 hours without food. The time for fifth instar larvae was approximately 120 hours, presumably because of the differences in physiology and the nearness to pupation. Fifth instar larvae also appeared to be diseased whereas fourth instar larvae showed no signs of disease. Their ability to migrate over distances then depends on their state of health and tolerance of starvation.

Smythe: How readily can we translate certain levels of defoliation into a decrease of either nut or wood production?

Farris: You are getting into an area with which I am not familiar. Perhaps someone else can answer that.

Nicholls: There have been several studies on insect defoliation of conifers, something like 170 studies, which showed that defoliation is proportional to the amount of fiber loss. In other words, with 50 percent defoliation of a tree, there is approximately 50 percent fiber loss. I don't know how defoliation relates to deciduous trees but Ken Kessler is planning to do some work on that aspect this summer.

Payne: On pecans, aphid infestation has been related to nut loss, but in the following year's crop. The aphids were affecting mainly return bloom on the Persian walnut in California and on southern pecan in Georgia.

Farris: In 1941 a researcher named Dickson showed that several years of defoliation of black walnut caused the nut kernel to decrease each year. By the end of the third or fourth year of defoliation, little kernel was left.

McPherson: I have two questions. One, is the walnut caterpillar ever trivoltine in southern Illinois?

Farris: It might be possible if weather conditions were right. A very warm spring and a long, warm fall may be suitable for a third generation. I have no proof but I believe that the key to a second generation may be in the amount of light to which newly hatched, first generation larvae are exposed. In May there is probably enough light to trigger the physiological mechanisms for development to proceed. In most years, however, temperatures do not reach the 80° level required for completion of the first generation until sometime into June.

McPherson: I have a second question concerni something I have always been curi about but have never investigated When these animals migrate from one tree to another, do they migr in mass or do they just sort of filter over?

Farris: I have observed 3rd, 4th, and 5th instar larvae leaving trees and th just scattered in all directions. At first I thought perhaps light was influencing the direction in which they were traveling but lat I found them on the north as well as on the south, east and west sides of trees.

McPherson: Do they all leave the tree at the same time?

Farris: No, they leave over an extended period of time.

A PRELIMINARY REPORT ON THE BIONOMICS OF FULGOROIDEA ON BLACK WALNUT WITH EMPHASIS ON ANORMENIS SEPTENTRIONALIS (SPINOLA) (HOMOPTERA)

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and

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ABSTRACT:--Preliminary findings from a study of the bionomics of Fulgoroidea occurring on black walnut are presented, including a generalized life cycle for Anormenis septentrionalis.

Nixon and McPherson (1977) reported collecting 15 fulgoroid species on black walnut in southern Illinois, 11 of which were noted feeding (Table 1). However, the impact of these species on walnut was not determined. The purpose of the present study is to determine if the abovementioned fulgoroids are reproducing on black walnut, or are incidental feeders.

Table 1.--A list of the Fulgoroids collected from black walnut trees in southern Illinois (Nixon 1976)

Family/ species	Feeding observations
Cixiidae	
Cixius sp.	
Haplaxius pictifrons (Stal)	
Oliarus sp.	
Delphacidae	
Liburniella ornata (Stal)	X
Derbidae	
Anotia bonnetti Kirby	X
Apache degeerii (Kirby)	X
Cedusa kedusa McAtee	X
Syntames uhleri (Ball)	X
Flatidae	
Anormenis septentrionalis (Spinola)	X
Metcalfa pruinosa (Say)	X
Ormenoides venusta (Melichar)	X
Acanaloniidae	
Acanalonia bivittata (Say)	X
Acanalonia conica (Say)	X
ssidae	
Thionia bullata (Say)	
Thionia simplex (Germar)	X

During 1976, 1977, and spring 1978, collection trips were made primarily to the following walnut plantations in southern Illinois: U.S. Forest Service Tree Improvement Center (T9S R2W S25), Indian Creek Walnut Plantation (T10S R1W S25), and a plantation located near the Swine Center on the SIU-C campus (T9S R1W S31). Other plantations visited included the Union County Tree Farm Walnut Plantation (T12S R2W S8) and a private plantation in Okawville (T1S R5W S13). More complete descriptions of these plantations are given by Nixon and McPherson (1977).

Fulgoroids collected as adults, thus far, include: Liburniella ornata (Stal), Anormenis septentrionalis (Spinola), Metcalfa pruinosa (Say), Ormenoides venusta (Melichar), Cedusa kedusa McAtee, and Acanalonia bivittata (Say). Only 2 species, M. pruinosa and A. septentrionalis have also been collected as immatures, suggesting that the remaining 4 species are incidental feeders.

M. pruinosa appears to be univoltine. Nymphs have been collected on black walnut from 9 to 19 July, adults from 5 to 18 September. Eggs have not been found, but probably represent the overwintering stage. Data from other southern Illinois host plants are more complete and also indicate that this species is univoltine.

A. septentrionalis has proven to be the most common fulgoroid on black walnut in southern Illinois and has been found to breed on this host plant as well as others. The rest of this report concentrates on this species.

A. septentrionalis occurs over much of the eastern U.S. (Metcalf 1923, Van Duzee 1923, Swain 1948). It has been collected in Connecticut, New York, New Jersey, Maryland, District of Columbia, Pennsylvania, Virginia, North Carolina, South Carolina, Georgia, Florida, Mississippi, Tennessee, Ohio, Indiana, Illinois, Iowa, Kansas and Arizona (see Metcalf 1957) and is common throughout its range (Southwick 1892, Swain 1948). Walden (1922) noted high populations in 1921 in Connecticut.

A. septentrionalis has been noted feeding on shrubs and woody vines (Swain 1948), especially on shoots and midribs of leaves (Comstock 1940), and collected from over 30 species of plants (Table 2). It has been implicated in foliage damage to *Cornus asperifolia* (of authors not Michaux) (= *Cornus drummondi* Meyer) (Swezey 1903) and was thought to be involved in the transmission of blueberry stunt disease until this was disproven by Tomlinson *et al.* (1950).

A. septentrionalis breeds on many shrubs and vines (Dozier 1928). The eggs have been found in several woody plants (Table 3) and the ovipositional damage has been described (Hoffmann 1942). Laboratory reared animals during the present study have laid eggs in the fleshy tissue of snap beans (*Phaseolus vulgaris* L.).

The first report of an association of *A. septentrionalis* with black walnut in southern Illinois was by Nixon and McPherson (1977) who found eggs, nymphs and adults on this host plant. During the course of the present study, black walnut twigs containing *A. septentrionalis* eggs have been found at the following southern Illinois locations: The La Rue-Pine Hills Ecological Area, Thompson Woods on the SIU-C campus, a private walnut plantation in Okawville, and the U.S. Forest Service Tree Improvement Center, SIU-C.

The following generalized life cycle information for *A. septentrionalis* includes data fro black walnut and other host plants (see SWW/JEM Table 2). The eggs are laid in the fall (earliest collection date, 5 September), overwinter, and hatch in spring. They are inserted into twig tissue in one or more rows. A typica row has a zipper-like appearance with the eggs forming a ridge on the surface of the twig (Figure 1). A search for eggs in black walnut twigs at the Tree Improvement Center during fall 1977 resulted in 316 in 16 different twigs (mean number of eggs per cluster ± 1 S.E. = 19.75 ± 2.44). The eggs were found within localized areas of the plantation (Figure 2).

First instars (Figure 3A) have been found from 23 May to 1 June; second instars (Figure 3B), 25 May to 6 June; third instars (Figure 3C), 25 May to 6 June; fourth instars (Figure 3D), 26 May to 30 June; fifth instars (Figure 3E), 8 June to 29 July; and adults (Figure 4), 23 June to 28 October.

ACKNOWLEDGMENTS

We wish to thank D. T. Funk and B. C. Webe Forestry Sciences Laboratory, North Central Forest Experiment Station, U.S.D.A., Carbondale Illinois, for their willing assistance during this study.

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Table 3.--A list of the oviposition sites of Anormenis septentrionalis

Common name	Scientific name	References
Hickory	*Carya* sp.	Dozier 1928
Black walnut	*Juglans nigra* L.	Nixon & McPherson 1977 SWW/JEM[1]
Sweetgum	*Liquidambar styraciflua* L.	Dozier 1928
Black cherry	*Prunus serotina* Ehrhart	SWW/JEM
Oak	*Quercus* sp.	Dozier 1928
American elm	*Ulmus americana* L.	Hoffmann 1942
Redbud	*Cercis canadensis* L.	SWW/JEM

[1] SWW/JEM = this study

Table 2.--A list of the plant associations of Anormenis septentrionalis

Common name	Scientific name	Stage[1]	Feeding	References
Maple	*Acer* sp.			Heaton 1934
Silver maple	*Acer saccharinum* L.	A	X	SWW/JEM[2]
Black alder	*Alnus glutinosa* (L.)		X	Dozier 1928
			X	Osborn 1938
Crossvine	*Bignonia capreolata* L.		X	Dozier 1928
Pignut hickory	*Carya glabra* (Miller)	A	X	SWW/JEM
Pecan	*Carya illinoensis* (Wangenheim)		X	Dozier 1928
Climbing bittersweet	*Celastrus scandens* L.	N	X	Swezey 1903
			X	Dozier 1928
			X	Osborn 1938
Redbud	*Cercis canadensis* L.	A	X	SWW/JEM
Roughleaf dogwood	*Cornus drummondi* Meyer	N	X	Swezey 1903
Flowering dogwood	*Cornus florida* L.	A	X	SWW/JEM
Dogwood	*Cornus* sp.		X	Dozier 1928
			X	Osborn 1938
Hawthorn	*Crataegus* sp.	N	X	Swezey 1903
			X	Dozier 1928
			X	Osborn 1938
American beech	*Fagus grandifolia* Ehrhart			SWW/JEM
Ash	*Fraxinus* sp.			Heaton 1934
Honey locust	*Gleditsia triacanthos* L.			Heaton 1934
Black walnut	*Juglans nigra* L.	N	X	Nixon & McPherson 1977
		A	X	SWW/JEM
Sweetgum	*Liquidambar styraciflua* L.	A	X	SWW/JEM
				Dozier 1928
Yellow sweet clover	*Melilotus officinalis* (L.)	N	X	SWW/JEM
Red mulberry	*Morus rubra* L.	N	X	SWW/JEM
Hophornbeam	*Ostrya virginiana* (Miller)	A	X	SWW/JEM
Pokeweed	*Phytolacca americana* L.			Dozier 1920
American sycamore	*Platanus occidentalis* L.			Heaton 1934
				SWW/JEM
Black cherry	*Prunus serotina* Ehrhart	N	X	SWW/JEM
		A	X	SWW/JEM
Plum	*Prunus* sp.	N	X	Swezey 1903
			X	Dozier 1928
			X	Osborn 1938
Red oak	*Quercus rubra* L.	N	X	Swezey 1903
			X	Dozier 1928
			X	Osborn 1938
Willow	*Salix* sp.			Heaton 1934
American elm	*Ulmus americana* L.			Gibson 1973
Slippery elm	*Ulmus rubra* Muhlenberg	N	X	SWW/JEM
		A	X	SWW/JEM
Elm	*Ulmus* sp.			Heaton 1934
Blueberry	*Vaccinium* sp.	A	X	Tomlinson *et al.* 1950
Verbisina	*Verbisina*			SWW/JEM
Grape	*Vitis* sp.	N	X	Swezey 1903
				Wirtner 1905
			X	Dozier 1928
				Heaton 1934
			X	Osborn 1938
				Comstock 1940
Prickly ash	*Xanthoxylum americanum* Miller	N	X	Swezey 1903
			X	Dozier 1928
			X	Osborn 1938
Corn	*Zea mays* L.			Heaton 1934

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[1] A = Adult, N = Nymph

[2] SWW/JEM = this study

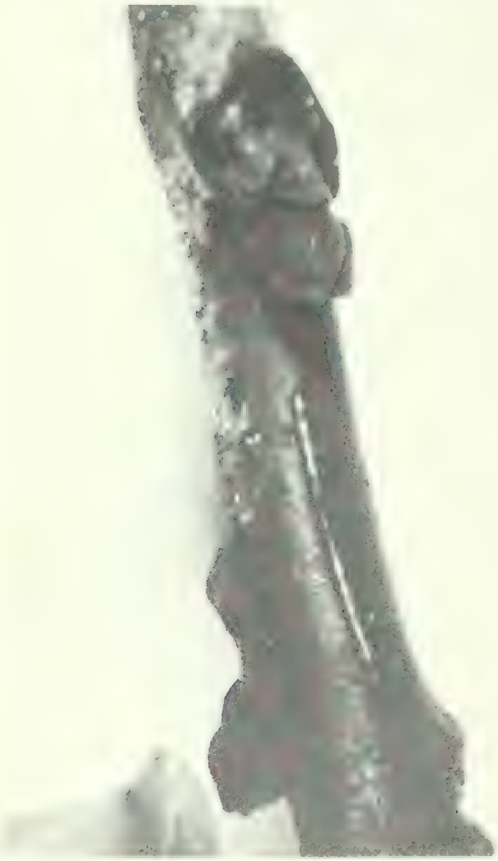

Figure 1.--Eggs of A. septentrionalis inserted in a black walnut twig.

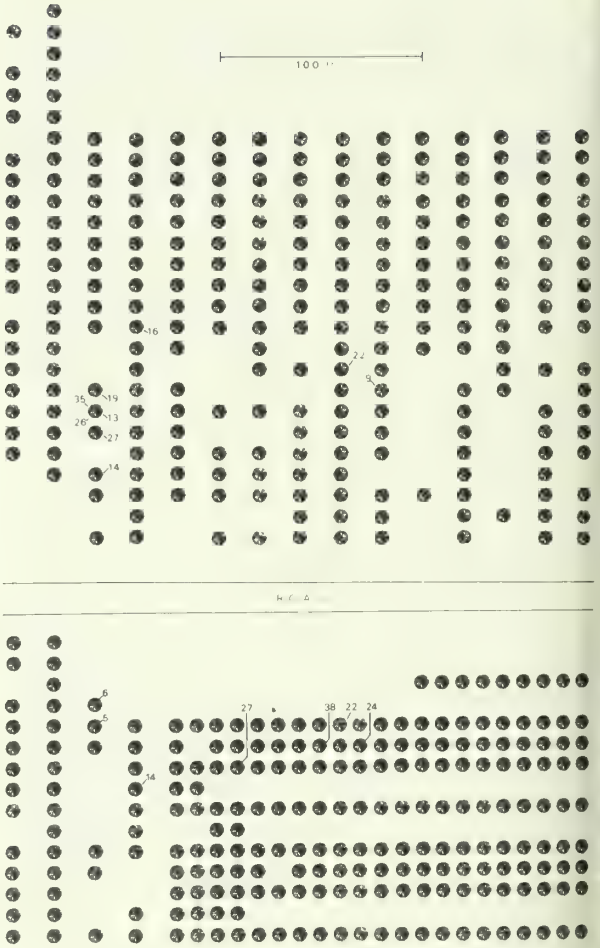

Figure 2.--Distribution of A. septentrionalis ovipositional sites at the U.S. Forest Service Tree Improvement Center Walnut Plantation, SIU-C. Numbers indicate the number of eggs in a twig.

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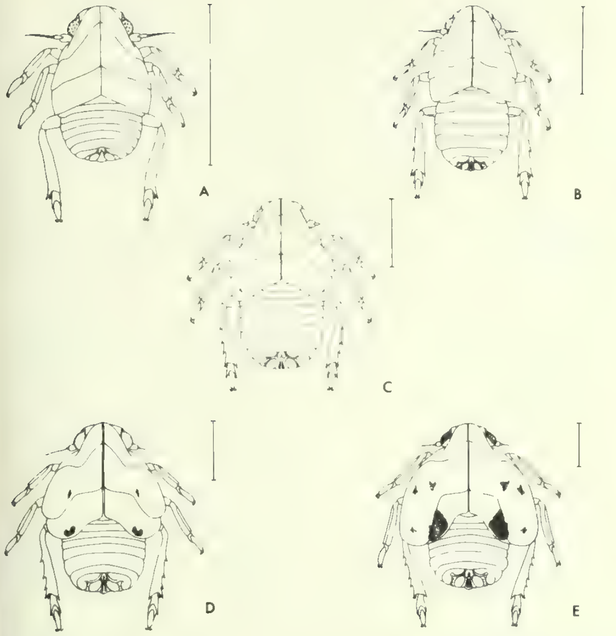

Figure 3.--Immature stages of A. septentrionalis. A, first instar; B, second instar; C, third instar; D, fourth instar; E, fifth instar. Line equals 1.0 mm.

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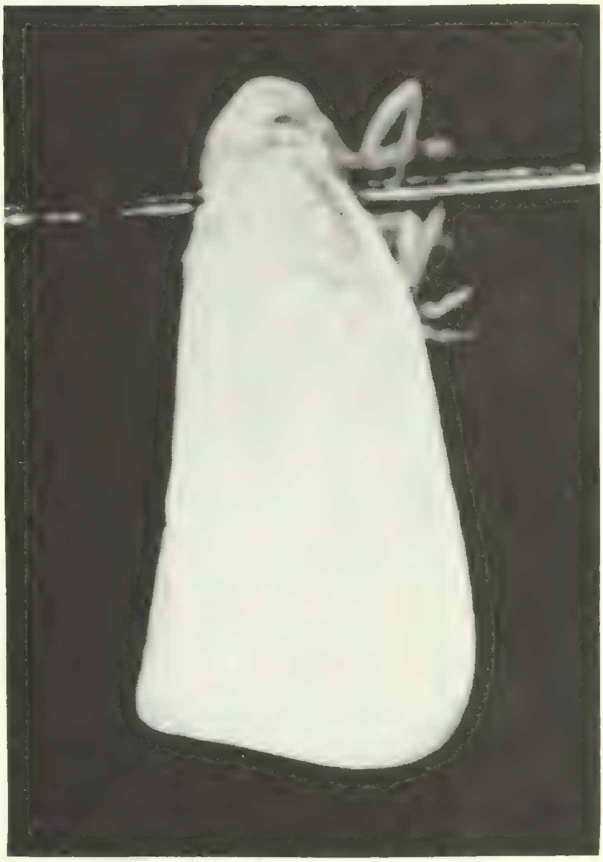

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GROUP DISCUSSION

Kuntz: Have you determined that these chocolate brown lesions, either on the leaves or the twigs, are a result of the activities of these insects?

S. Wilson: No, I haven't to date. We have tagged twigs in the field in which there have been eggs, and we will follow them this year. Of all the ones that were tagged last year only one twig failed to leaf out and there may have been other causes.

Schlesinger: Do they lay their eggs in last year's wood?

Wilson: No, I have observed eggs only in the current year's growth. Oviposition damage from previous years is evident on the twigs, but I've found fresh eggs on the current year's growth only.

THE BUTTERNUT CURCULIO ON SOME HYBRID WALNUTS IN MICHIGAN

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ABSTRACT.--Susceptibility of several species and hybrids of walnuts to attack by the butternut curculio is given and injury classes are proposed. Progeny from a J. nigra X J. sieboldiana cross were most susceptible to attack.

The butternut curculio, Conotrachelus juglandis LeConte, attacks native and exotic species of natural and planted Juglans in eastern North America. The larvae and adult weevils injure or destroy the nuts, young stems, and leaves of their hosts, and thus curtail nut production and modify tree growth and form. The life history of this insect has been studied in Connecticut (Britton and Kirk 1912) and in West Virginia (Brooks 1922). Its range, however, extends throughout Eastern North America--contiguous with the natural range of butternut, its native host.

In 1975, we found the butternut curculio attacking the shoots of several hybrid Juglans in a research planting at the Kellogg Forest near Augusta, Michigan. The apparent wide range of attacks suggested a wide range of susceptibility. Some of these trees may eventually be used for seed selection due to their superior growth or nut production, so we undertook this study to determine: (1) the insect's life history in Michigan, (2) the degree of susceptibility of walnut trees to weevil attack, and (3) the degree of feeding damage impact.

STUDY AREA

The study area was a putative hybrid walnut plantation (compartment 20A) of the Kellogg Forest, Kalamazoo County, Augusta, Michigan. The plantation was established in 1968 and consisted of open-pollinated progeny of the following species and hybrids: Juglans nigra (black walnut), J. cinerea (butternut), J. regia (English walnut), J. sieboldiana Japanese walnut), J. nigra X J. sieboldiana, J. regia X J. nigra, and J. sieboldiana X J. cinerea. The J. nigra was planted in part as a buffer along two edges of the plantation. Also, a large J. nigra provenance planting was adjacent to the hybrid plantation.

The trees were arranged in a randomized block design with eight replicates comprising 26 seed sources (Funk 1971). Each block consisted of five trees planted 10 feet apart in a row.

METHODS

The life history was studied in 1975 and 1976 from field observations and branch samples collected each week throughout warm weather (Corneil and Wilson 1978). Host susceptibility was determined by evaluating the degree of larval attacks and adult feeding on samples of each hybrid. In 1975 and 1976, each tree in the planting was scored attacked or not attacked and the percentage calculated for each replicate and each hybrid. In 1976, an injury index was developed for each hybrid to get a better estimate of the degree of attack. The index was based on the degree of attack on each tree and the percentage of trees attacked (Wilson et al. 1978). Indices between hybrids were contrasted using Scheffe's method of multiple comparisons for significant (0.05 level) differences.

LIFE HISTORY AND HABITS

Conotrachelus juglandis is univoltine in Michigan. The adult is the overwintering stage and it may live for a full year or longer.

In Michigan oviposition begins about the second week of May and continues until early August. The female weevil oviposits one egg in each niche she chews in the young shoots. Each niche is flanked on three sides by a crescent-shaped slit, which prevents the egg from being crushed by rapidly growing plant tissue (Porter 1932). A flap of tissue usually conceals the egg, and frass pellets sometimes plug the niche opening.

First-instar larvae appear in mid May about 6 to 12 days after oviposition, depending on the temperature (Britton and Kirk 1912). Each small larva bores into the pith and feeds up or down the stem or into the bases of the leaf petioles. The pith is soft and green at this time. As the larva grows it makes a larger and longer tunnel and is restricted only by the pith diameter of the shoot and petioles. Thus, oldest larvae are nearly always toward the shoot base where the pith diameter is largest, and youngest larvae are near the tip. Two or more larvae occupying the same shoot are able to completely bore out the center of the shoot. Larvae running out of food and reaching the base of the new shoot usually feed into the cambium and girdle the shoot there, and this is the major cause of shoot wilting and death. Partially hollowed-out shoots that do not break off usually survive.

During the larval growth period the egg-niche opening becomes the entrance to the larval tunnel and an ejection hole for frass. An active larval gallery has frass at the entrance and a darkened area of tissue encircling the opening.

There are five larval instars and the entire larval period lasts 4 to 6 weeks. When fully developed, the larvae exit through the tunnel opening and drop to the ground, usually during the early morning hours before heat of the day (Brooks 1922). Larvae begin dropping about mid June in Michigan and all have dropped by late August. The larvae then burrow into the soil as deep as 3 inches and construct small earthen pupal cells.

Pupation occurs 7 to 10 days after the larva enters the soil, and the pupal period lasts between 15 and 20 days. In Michigan the mean period from the time the larva enters the soil until the adults emerge is 27 ± 3 days. First adults appear in the second or third week in July and the last adults have emerged by mid September. Young adults fly to the host trees and feed on the soft tissues of the shoot tips, leaf rachis, and on the leaflets. Adults generally feed at night and rest on the foliage or hide during the day.

In autumn the adults drop to the ground, crawl beneath the litter, and burrow into the soil beneath the tree's canopy where they overwinter. In May they emerge, return to the tree, seek mates, and the females soon begin to oviposit. Adults feed on the soft, new shoot and leaf tissues throughout the summer and die in late summer or early autumn.

HOST SUSCEPTIBILITY

In general trees with Japanese walnut parentage were attacked the most by the weevil larvae; from 90 to 100 percent of the progeny were attacked in 1975 and 1976 on these hosts (table 1). Conversely black walnut was the least attacked--17 percent or less when planted among the hybrids. The adjacent walnut stand, which was a regional provenance planting of pure *J. nigra*, was not attacked.

The progeny from the *J. nigra* X *J. sieboldiana* parent sustained significantly higher injury and was 10 times more susceptible than black walnut (table 1). Progeny from *J. sieboldiana* were the second most injured, and those of *J. regia* X *J. nigra* and *J. sieboldiana* X *J. cinerea* were third. Both the *J. sieboldiana* and the *J. nigra* X *J. sieboldiana* progeny were 100 percent attacked by the weevil, yet the latter had almost twice as much injury. *J. regia* and *J. cinerea* were injured about the same as black walnut and these three together were ranked the lowest in susceptibiltiy. *J. regia*, however, had a much higher percentage of trees attacked than the others--a range of 71 to 95 percent, compared to 42 to 48 percent for *J. cinerea* and 15 to 17 percent for *J. nigra*.

Adult feeding ranked almost parallel to the larval feeding intensity but the differences between them were far less. The *J. nigra* X *J. sieboldiana* progeny had more than four times as many feeding wounds and *J. sieboldiana* had two times as many feeding wounds as *J. nigra*, *J. cinerea*, or *J. regia*.

DISCUSSION

The life history and habits of *C. juglandis* in Michigan are similar to those recorded for Connecticut (Britton and Kirk 1912) and West Virginia (Brooks 1922), except the life cycle begins a few weeks earlier and ends a few weeks later in Michigan.

Table 1.--Susceptibility and injury to various walnut progeny by the butternut curculio, 1975-1976

Juglans - Female Parent (Male open-pollinated)	Seed Sources (No.)	Progeny Trees (No.) 1976	Tree Mean Height (m) 1976	Trees Attacked (%) 1975	Trees Attacked (%) 1976	Mean Injury Index (I) 1976[1]
J. nigra X J. sieboldiana	1	20	4.4	100	100	24.0 a
J. sieboldiana	1	14	5.6	100	100	14.3 b
J. sieboldiana X J. cinerea	7	243	4.8	90	90	8.9 c
J. regia X J. nigra	4	57	2.7	88	81	7.8 c
J. regia	1	19	2.1	95	71	4.3 d
J. cinerea	2	55	4.7	42	48	2.8 d
J. nigra (within stand)	10	41	4.8	15	17	2.3 d
J. nigra (adjacent stand)	10	160	4.9	0	0	0 e

[1] Indices followed by the same letter are not significantly different at the 0.05 level.

The main injury from C. juglandis to walnuts is from larvae tunneling in the pith and girdling the base of the new shoots. Tunneling weakens the shoot so growth is slowed or so they eventually break from wind or snow. Girdling kills the shoot by severing the cambium, and because most girdling occurs near the base of the new shoot, most or all of the season's growth is lost.

Adult injury occurs mostly during spring feeding when the shoots are small and succulent. Then feeding niches may cut through half of the shoot's diameter and cause it to wilt and die. After mid-June damage is less serious because the shoots are larger. Fall feeding following new adult emergence causes numerous feeding wounds along the shoot, but these scar and callous usually without injuring growth or form. Adults also heavily skeletonize the leaflets. Feeding wounds on leaf petioles in the fall kill an occasional leaf but natural leaf fall occurs shortly thereafter anyway.

Britton and Kirk (1912) ranked several species of Juglans attacked by the butternut curculio in the following preferred order: J. cordiformis, J. sieboldiana, J. cinerea, J. regia, J. nigra, and J. mandschurica (manchurian walnut). Brooks (1922) noted that J. cathayensis (Cathay walnut) was sometimes seriously injured by this weevil and was perhaps about as susceptible as the Japanese walnuts.

Host preference ranked similarly in our study excluding progeny from J. mandschurica and J. cathayensis, which were not available for comparison. Progeny with Japanese walnut parentage were highly preferred over the other exotic and native hosts. Black walnut appeared to have little or no effect on the susceptibility to attack when crossed with other walnuts, whereas butternut seemed to decrease susceptibility when crossed with Japanese walnuts.

Although English walnut ranked about the same as butternut and black walnut, it still may be slightly more susceptible than expected. English walnut trees grew poorly in Michigan and each year their shoot tips were killed back by late frost. Those that had not died in the study plots were short, deformed, and bushy. Presumably, few available shoots were available for weevil attack after each spring frost. An indication that they might be more susceptible is reflected perhaps in the J. regia X J. nigra cross, which had significantly higher injury than J. regia or J. nigra alone. The progeny from this parent had less frost injury each spring than the English walnuts and thus more shoots available for attack. Because J. nigra is barely susceptible and does not seem to contribute much to susceptibility in other crosses, the J. regia component in this cross most likely contributed the additional susceptibility. This may be important for future crosses or further south of the latitude of Michigan where English walnut might be planted.

Black walnut either lacks a substance that attracts the weevil or contains a substance that repels them. Extensive observations in the walnut provenance planting, which was adjacent to the hybrid planting, indicated the adult weevils only nibbled a small amount on the trees. Oviposition was extremely rare and no larval tunnels were found, confirming black walnut as an extremely poor host (Britton and Kirk (1912) and Porter (1932) have also reported that black walnut is seldom attacked by C. juglandis).

Butternut was not much more susceptible to injury by the weevil than black walnut, though there was a slightly higher percentage of trees attacked. Native butternut is the weevil's principal host in natural situations, so perhaps natural selection has favored this tree's resistance.

The degree of shoot injury observed on the various hosts in this study suggests four injury classes J. nigra, J. cinerea, and J. regia are in the Very Low Class. Such trees have no more than 0.5 weevil attacks per shoot. Sparse and widely scattered shoot and leaf flagging (wilting) occurs on them and damage at most is slightly cosmetic. J. sieboldiana X J. cinerea and J. regia X J. nigra are in the Low Class and have approximately 0.5 to 1.0 attacks per shoot. These trees show scattered shoot flagging and the few trees that are killed have multiple attacks on the same shoot. J. sieboldiana are in the Moderate Class and have 1 to 3 attacks per shoot. Shoot and leaf flagging readily occurs throughout the tree's crown but is widely scattered. Some lateral and an occasional leader shoot are killed back at this density. Tree form is affected mostly where attacks on leaders occurs two or more years in a row. J. nigra X J. sieboldiana are in the High Class. These have more than three attacks per shoot, and many shoots are hollowed out for more than 30 percent of their length. Heavy wilting occurs to shoot tips and leaves. Many shoots die--less than half of the injured shoots recover the year following attack. Trees with the amount of injury in the High Class category will usually warrant suppression measures.

No attempt has yet been made to suppress the butternut curculio. However, its life history is similar to the black walnut curculio, C. retentus (Say), so similar suppression measures are plausible. Both weevils appear to be suppressable in the adult stage--either while feeding in late summer and autumn following emergence or in the spring after overwintering. Jaynes (1969) recognized fall spraying as a potential time for C. retentus control. The adults feed for more than a month in the fall so there is a good chance they will eat or contact any persistent pesticide. Gibson and Kearby (1975) obtained fair suppression of C. retentus adults during the beginning of feeding and oviposition. Similar techniques should be tried on the butternut curculio.

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GROUP DISCUSSION

Weber: I would like Dave Funk to comment on the cross between Juglans cordiformis and nigra as to its importance as a hybrid tree.

Funk: I think this is perhaps the most promising cross we have. I fooled around with walnut hybrids quite a bit and am rather well discouraged with the whole program, but the cordiformis X nigra cross is rather vigorous and might be a pretty good dual-purpose tree.

L. Wilson: I would like to mention that the people in Connecticut (Britton and Kirk) rank their trees almost identically to some of the crosses in our study. Pure cordiformis is highly preferred by the butternut curculio. In our study my only question was that nigra did not seem to knock down any of the resistance whereas cinerea did knock back the resistance to some extent. That's the only thing I could see from the data that made sense to me. As a geneticist, maybe you see something different.

Funk: I think that is a fairly limited sample of what the species might produce. We're looking at individual parents.

Wilson: I realize that but at least the parallels were identical. They were in the same order of preference with almost no differences. If there were, they were just reversed by number but not be significance. J. cordiformis seems to be the most susceptible species that we've tested. Mandshurica was brought in, too, as a fairly susceptible species.

THE LIFE HISTORIES OF ACROBASIS JUGLANDIS AND A. DEMOTELLA ON BLACK WALNUT IN MICHIGAN

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ABSTRACT.--Describes the life histories of two walnut pests: one a shoot borer and the other primarily a defoliator. Some control recommendations are proposed.

At least two pyralid moths, Acrobasis juglandis (LeBaron) and A. demotella Grote are injurious to young black walnut, Juglans nigra L., trees in Michigan. A. juglandis, the pecan leaf casebearer, is well known in the southern United States as a severe defoliator of pecans (Bissel 1942, Gill 1917, Nickels 1951), but except for studies in Missouri (Kearby 1975) little is known of its biology in the northern United States on walnut. A. demotella, the walnut shoot moth, has had less attention (Hulst 1890, Neunzig 1972, Kearby 1975) until recently when Kearby (1978) reported on its biology and injury in Missouri. In 1975, we began a study on the life histories of both species in Michigan.

METHODS AND MATERIALS

This study was conducted during 1975 and 1976, in a 6-acre black walnut plantation in Branch County, and in a 20-acre mixed woodlot and old field in Clinton County, Michigan. Additional data were collected from walnut plantings in Shiawassee, Clare, Livingston, and Kalamazoo Counties. Sample trees were less than 15 cm d.b.h., 10-15 years old, and under 6 m tall.

Insect specimens were collected one or more times each week. Some were fixed in KAA and then transferred to 80 percent ethanol for head capsule measurements. Several larvae were reared in the laboratory on potted walnut seedlings. Adults were reared from late-stage larvae in Deitz globes covered with fine-mesh cloth. Adults were captured with light traps after emergence in the field.

LIFE HISTORY AND HABITS

Both A. juglandis and A. demotella are univoltine in Michigan (fig. 1). Each species undergoes five larval stages. The larvae are difficult to distinguish in the first three instars as their size, head capsule measurements, and setal patterns are similar. In the fourth and fifth instars however, A. demotella is larger than A. juglandis as follows:

Species	Instar	No. head capsules	Mean width (mm)	Range (mm)
A. juglandis	IV	14	0.775	0.644 - 0.993
	V	24	1.214	1.043 - 1.373
A. demotella	IV	8	0.981	0.948 - 1.098
	V	20	1.448	1.299 - 1.610

Martinat (1978) and Kearby (1978) give further details on separating these species by morphology and behavior.

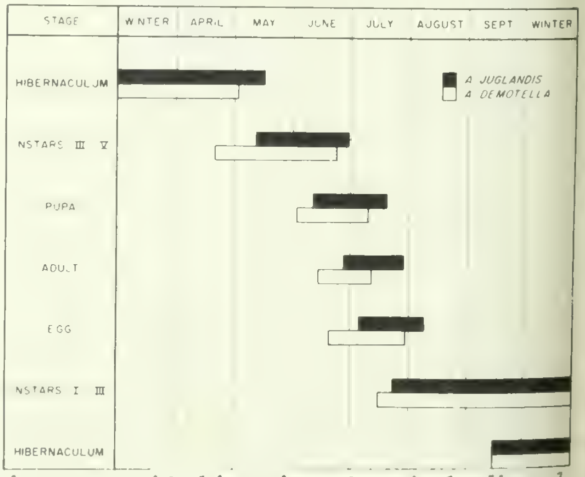

Figure 1.--Life histories of A. juglandis and A. demotella on black walnut in Michigan.

Egg Stage and Larval Instars I-III of A. juglandis and A. demotella

Oviposition starts in the latter half of June for A. demotella and early July for A. juglandis (fig. 1). Eggs are deposited singly on the underside of the leaves, usually next to the midrib on the basal half of the leaflet. Turner et al. (1978) and Leiby (1925) found up to 30 eggs in a single leaflet on pecan. No leaflet was found with more than two eggs in Michigan; 40 percent of the egg-bearing leaflets had two eggs, 60 percent had one.

The eggs fit Gill's (1917) description of those of A. juglandis. They are elliptical, ivory white, convex above, and flattened below, with a reticular micro-pattern on the outer surface of the chorion. Vacated eggs are colorless and usually collapsed with a round exit hole at one end. The average size of ten eggs was 0.28 x 0.71 mm. Eggs laid in the lab from field-collected A. demotella adults were similar in appearance and size to those of A. juglandis. The incubation period for lab-oviposited A. demotella eggs averaged 11 days.

Larvae appear in late July. First instars of both species are pale reddish brown and about 0.8 mm long. Shortly after eclosion they wander a short distance from the egg shell and begin constructing a sinuous trumpet-shaped case of frass on a silken framework. The larvae from the first to the third instars feed on the lower epidermis, skeletionizing the leaflet in the vicinity of the case. When foliage starts to discolor in mid-to late September, the third instar larvae vacate the cases and move to the nearest shoots and construct oval brown hibernacula that are approximately 1 mm long. These are usually concealed at the base of the buds. There the larvae overwinter.

ate Larval Instars, Pupae, and Adults of A. juglandis

Third instar larvae of A. juglandis merge from their hibernacula in the spring, egin feeding at the base of the terminal bud, nd conceal themselves beneath loose, silken, rass-coated webbing. Emergence varies with ifferences in spring temperature. Active arvae were first observed on May 12, 1975, nd on April 30, 1976. The larvae continue to eed at the base of the bud for several weeks d throughout third instar development. Some ds are killed, but most expand and foliate ormally.

The fourth instar moves to the expanding leaf and constructs a silken frass-coated case attached to the rachis, usually near the terminal pair of leaflets. The case is enlarged as the larva grows and adjacent leaflets are pulled together, fastened with silk, and fed upon. The last instar larvae feed on the bases of the leaflets and rarely leave their cases. Fully mature larvae seal the ends of the cases and await pupation.

The first pupae appear near mid-June; the entire pupal period may last until mid-July. A. juglandis pupae reared in the laboratory averaged 16.3 (12-24) days to develop to adults.

Adults emerge from the cases in late June. Adults were observed in Branch County between June 26 and July 18--the peak occurred from July 11-14. In Shiawassee County (80 miles further north) they were seen from June 25 to July 27 with the peak between July 14-16.

Late Larval Instars, Pupae, and Adults of A. demotella

Third instar larvae of A. demotella emerge from their hibernacula in late April or early May depending on the weather. The larvae feed at the base of the bud, similar to those of A. juglandis, concealed in a silken web. The habits are sufficiently different, however, to distinguish them at this stage (Kearby 1978). As the larvae reach the fourth instar they tunnel into the newly developing shoots. Most enter the shoot in the axils between the shoot and the leaf petiole. Larval tunnels may reach 45 cm long; their openings are concealed with frass and silk. Both fourth and fifth instars tunnel in the shoot. Hollowed-out shoots invariably wilt and die.

Near the end of May or beginning of June the last instar larvae start vacating the shoots, drop to the ground, and burrow a short distance into the soil beneath the tree. There, they form a pupal cell, and await pupation. First pupae appear in early June, and the pupal period lasts about 16 days. Adults emerge after mid-June. Trapped adults were collected in Branch County from June 23 to July 15 with the peak between June 26-29; and in Shiawassee County from June 20 to July 28, with the peak around June 25-26.

DISCUSSION

The life histories of A. juglandis and A. demotella are similar but most stages of A.

demotella occur 1-2 weeks earlier in Michigan. Both have similar habits in the early larval instars, but considerably different habits in the last two instars. Their closely parallel life histories and similar habits suggest that they probably were sibling species. Initial geographic separation followed by subsequent overlap of ranges for example, could have led to late instar competition and divergence in habits. Studies made on other species of *Acrobasis* (Balduf 1966, Walley 1954, Wilson 1970, Pierce and Appleby 1973) suggests that this may have occurred many times in the genus. Wilson (1970) for example, stated that *A. comptoniella* and *A. rubifasciella* are nearly morphologically identical in the adult stage, but have distinct behavioral differences in the larval stages—a classic case of sibling species.

The highly divergent habits of these insects in the last-larval stages has brought about two distinct types of injury to the tree: shoot destruction and defoliation. Because *A. demotella* is a shoot borer, and because just one larva can kill a shoot or leader and cause a crooked tree, it is the more serious threat to walnut in Michigan. It is also the most destructive shoot borer in Missouri (Kearby 1978). *A. juglandis* normally causes only a small amount of growth loss or injury from its defoliation. Populations of *A. juglandis* would have to be several times more numerous to cause damage equal to *A. demotella*. Our light-trap catches of adults produced five *A. demotella* to one *A. juglandis* during both years of study, suggesting *A. juglandis* may be poor competitor in the early stages. It ecloses later in the summer and also appears later in the spring and thus may find its niche occupied by *A. demotella*.

Actual degree of injury was difficult to assess in this study because neither insect population was very high. Populations of both increased somewhat in 1976 following an exceptionally mild winter in 1975 which probably lowered overwintering mortality. *A. demotella*, however, is potentially destructive if it affects the form-phase of walnut development. When buds were killed and shoots hollowed out, lateral buds grew and caused crooked and multiple branches. Suppression most likely will be needed for *A. demotella* when populations build up.

Martinat (1978) tested three systemic pesticides against both species. He tried aldicarb, carbofuran, and disulfoton granular applications in late April 1976. Mortality, however, was not sufficient to warrant recommendations, and he felt better suppression might have been obtained if applied earlier.

McKeague and Simmons (1978) tested acephate and methoxychlor as single bud sprays and whole tree sprays. Acephate was consistently 10 to 20 percent more effective than methoxychlor.

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GROUP DISCUSSION

Weber: Bill Kearby finds that even with the first 3 instars he can tell the difference between the two species--*juglangis* and *demotella*--by means of their habits. According to Kearby, *Acrobasis juglandis* never goes into the bud. It chews on the outside of the expanding leaf, whereas *demotella* bores into the bud immediately after it comes out of its hibernaculum.

Another comment concerning *Acrobasis* is that we are studying the genetic resistance of black walnut to *Acrobasis* attack. Several seed sources from the Midwest planted as a seed orchard are being tested. Results indicate that the average infestation rate is high, ranging from 20 percent in 1977 and 33 percent in 1978, and that there are seed source differences.

McPherson: Louie, are you sure you only have two species in Michigan?

Wilson: I recently heard that there is a third species in Wisconsin but I don't know anything about it.

McPherson: In southern Illinois we have found 3 or 4 species. I wonder if some of the foul-up in data could be in mixing species?

Wilson: That is a possibility. The third species in Wisconsin was found on nursery trees. I don't know its name but it was determined to be different from *juglandis* or *demotella*.

Payne: We've been told that the insect we collect from pecan is the pecan nut casebearer, *Acrobasis nuxvorella*. We don't even use *juglandis* anymore. You made a comment earlier that you wondered if the species we had in the South is different. Maybe the taxonomists wonder, too, but we have to rely on them for our identification.

Wilson: It bothers me when the same species is reported all the way from Wisconsin to here in southern Illinois.

Payne: A taxonomist in North Carolina named Neunzig has published a monograph on *Acrobasis*. All the specimens that we have sent to him came back identified as *nuxvorella*, the pecan nut casebearer. Therefore, we don't know if we have *juglandis* in Georgia.

Pecan growers in Mexico reported an outbreak of nut casebearer where it supposedly was not distributed. We collected specimens and found not only the nut casebearer, *nuxvorella*, but also one called the nursery casebearer. This last was a new one which has not been reported from Georgia.

McPherson: *Acrobasis latifasciella* is another one of the species we have here in southern Illinois.

Wilson: That's the big problem. Taxonomists can't straighten it out by doing all our work for us.

EFFECTS OF INSECTICIDAL AND CULTURAL METHODS TO REDUCE ACROBASIS SPP. AND FROST INJURY ON BLACK WALNUT[1]

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ABSTRACT:--Excessive forking of black walnut saplings was noted in several plantations in Southern Michigan. Acrobasis juglandis (LeBaron) and A. demotella Grote cause forks by feeding on walnut buds and shoots. Two insecticides, acephate and methoxychlor, were tested for effectiveness against these insects. Trials were conducted in the spring and fall. In each case, acephate and methoxychlor caused a significant reduction in both the damage and the number of insects, with acephate consistently 10 to 20% more effective. A single bud spray test conducted in the spring resulted in a greater reduction of Acrobasis damage than did whole tree spraying. Mortality resulting from the fall spray test was 60 to 80%.

Frost also plays a major role in damaging buds and shoots. In 1977, nearly 100% of the terminal buds were killed by the combined action of frost and Acrobasis larvae. As a corrective measure for both problems, pruning was tried. All but one of the new shoots on a damaged branch were removed in early summer. This pruning technique corrected forking effectively. In areas where frost is known to damage black walnut saplings, corrective pruning may be a more reliable method for preventing forking than is spraying an insecticide to control only Acrobasis spp.

Black walnut saplings with an unusually high proportion of killed terminal buds and forked branches were observed in several southern Michigan plantations (Figure 1). Insects, identified as Acrobasis juglandis (LeBaron) and Acrobasis demotella Grote (Lepidoptera: Pyralidae), were found feeding on walnut buds and shoots.

Two insecticides, acephate (Orthene) and methoxychlor, were tested for effectiveness against these insects. Tests were conducted in the spring and fall. During the evaluation of the spring spray test, another type of bud damage was noticed, which was caused by late frost. Since black walnut is growing at the northern limits of its range in Michigan, frost damage is likely to be a continuing problem. A pruning technique was tested for its effectiveness in reducing both insect and frost-caused injury. This paper briefly describes the insects' life history and damage and reports the results of these insecticide and pruning tests.

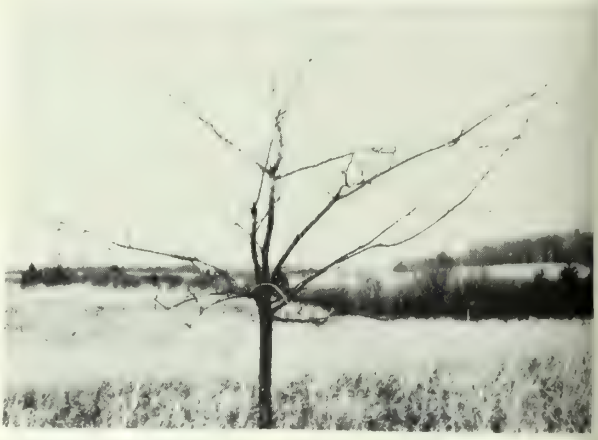

Figure 1.--Black walnut in Michigan with many killed terminal buds and forked branches.

THE INSECT AND ITS DAMAGE

Both Acrobasis juglandis and A. demotella (Lepidoptera: Pyralidae) have been found feeding on walnut in southern Michigan. They damage terminal growth of trees by feeding on expanding buds and shoots in the spring. Several authors have researched the life history of these insects (Gill 1917, Kearby 1975, Martinat 1975, Nickels 1951).

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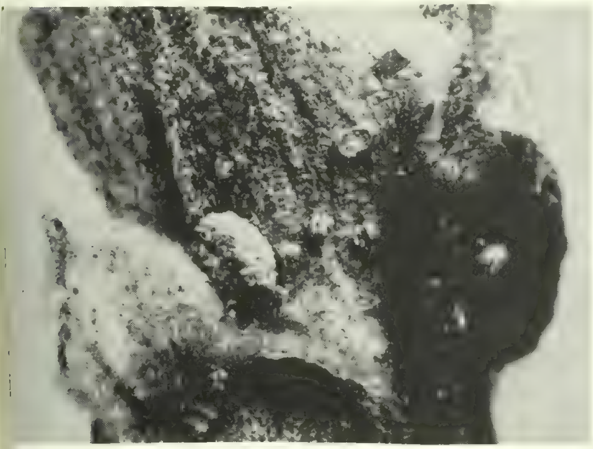
[1] Michigan Agricultural Experiment Station Journal Article No. 8595.

Larvae of both insects overwinter in small inconspicuous cases or hibernaculae on or near the buds (Figure 2). According to Kearby (1965), A. juglandis prefers lateral buds and A. demotella, terminal buds. The spring feeding habits of these two insects are very similar. The larvae emerge when buds burst and feed on the expanding buds. This feeding usually results in the death of the bud. A. juglandis continues to feed on opening buds or at the base of new shoots for several weeks. Some A. demotella larvae move to a partially grown shoot and begin boring into it. These tunneled-out shoots often wilt and die back to the previous year's growth.



igure 2.--Hibernacula of Acrobasis juglandis or Acrobasis demotella larvae on a walnut bud.

By early June, in Michigan, most A. demotella h've dropped to the ground to pupate. They pupate jst beneath the soil surface in an earthen cell (earby 1975). A. juglandis larvae have by this tme moved from the bases of shoots to the under-sles of leaves, where they build a silk and fass tube attached to the rachis (Figure 3). T leaflets on either side of the case are fatened around it. The larva free-feeds on thse and nearby leaflets. In mid June the larva cses the end of the case and pupates inside.

In 1975, Martinat collected A. demotella adlts from June 23 to July 15. The oviposition sie and behavior of early instars before over-witering are unknown at this time. The majority ofA. juglandis adults emerge 2-3 weeks later than A. demotella moths (Martinat 1975). Eggs are laid sigly on the undersides of leaflets (Gill 1917). Afer hatching, the larva moves a short distance an starts constructing a silk and frass case. Th larva skeletonizes the lower layer of the le. The case is extended in a serpentine paern as the larva grows (Figure 4). Necrosis

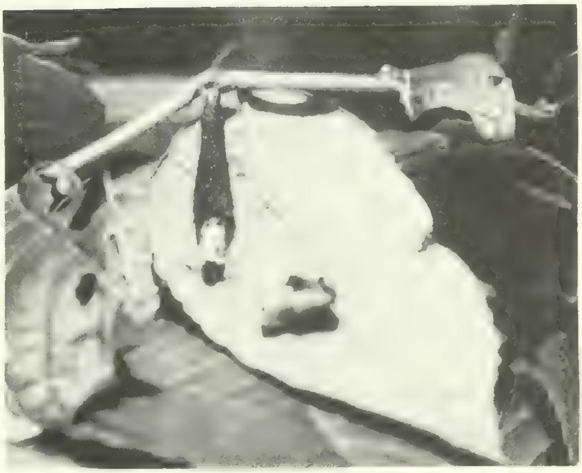


Figure 3.--Silk and frass case of late instar Acrobasis juglandis present in midsummer on the rachis of a walnut leaf.

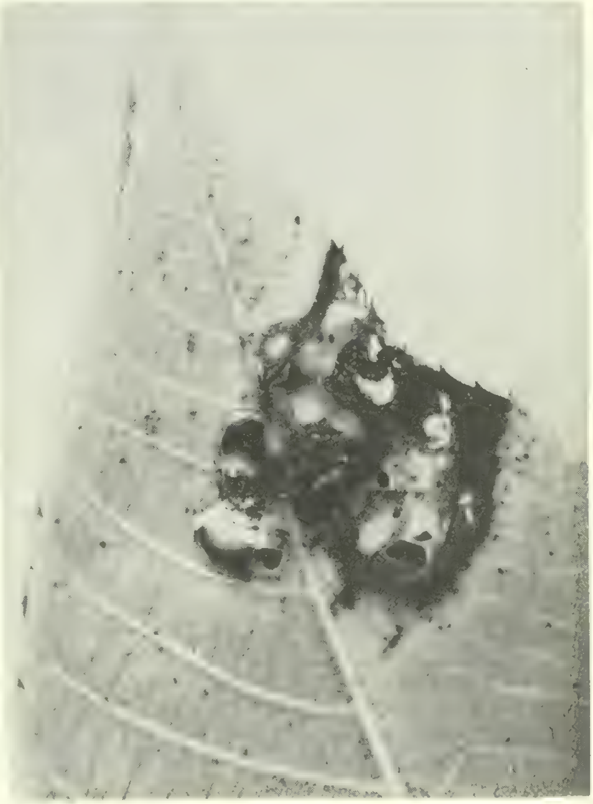


Figure 4.--Silk and frass case of early instar Acrobasis juglandis (or possibly A. demotella) on a walnut leaflet.

occurs where the leaflet has been skeletonized, giving them a blotched appearance. Just before leaf fall, larvae move to their overwintering sites near the buds.

MATERIALS AND METHODS (Insecticidal)

A 60 acre black walnut plantation located in Branch County near Quincy, Michigan, was chosen for this study. This plantation is particularly well suited to a study concerned with agents affecting tree form. Tree height ranges from 5 to 25 feet. During this phase, straight growth is crucial to the formation of clear wood in the first 16 ft. log of timber-producing black walnut trees.

Three spray tests were conducted using acephate and methoxychlor. Each treatment (acephate, methoxychlor, unsprayed) was applied to a block of 50 trees. Each block was separated by several rows of trees to minimize spray drift. Trees were sprayed with a 2 gal. hand sprayer using 2 to 3 tablespoons per gallon of each chemical. Trees 10 feet and under were chosen to facilitate spraying and data collection.

Two spray tests were conducted in early May. The trees were sprayed just prior to bud burst and emergence of early instar *Acrobasis* from their hibernaculae. In one plot, the entire tree, including branches and trunk, was wet down with spray mixture. In the other, only one terminal bud plus the branch were sprayed. Several weeks later, after larvae had begun feeding in the expanding buds and shoots, infested and uninfested buds per tree, plus those killed by frost, were counted. Any dead bud which had frass issuing from it, was counted as infested, although it may have been damaged by frost as well. A students' t test was used to compare post spray counts in sprayed and unsprayed areas.

Another part of the plantation was sprayed in September, a few weeks before leaf fall. At that time, *Acrobasis* larvae were free-feeding on the undersides of the leaflets. Spray was applied with a hand sprayer to the trees until the leaves were saturated. Just prior to spraying, counts of larvae and numbers of terminal buds per tree were taken. Post spray counts were conducted in May of the next year. Hibernaculae per terminal bud were counted. Percent mortality and confidence intervals were calculated, using Simmons and Chen's (1975) two-sample and four-sample methods for assessing insecticide efficacy.

RESULTS AND DISCUSSION

Efficacy data from the spring spray tests and the fall spray test suggest that both acephat and methoxychlor reduced the damage and numbers of *Acrobasis*. Of the two spray tests conducted in the spring, the treatment of single buds was about 10% more effective in reducing bud damage (Table 1). A single bud spray is more efficient because larvae move from hibernaculae to buds on the same branch. More thorough coverage of the bud may result from more careful spraying when only one branch tip is designated. Althoug the reduction of *Acrobasis* injury in sprayed blocks of the single bud test are greater, actual numbers of injured shoots are higher than in the whole tree spray test.

Acephate reduced *Acrobasis* injury on terminal buds by approximately 10% more than methoxychlor (Table 1). In this respect the fall spray data show results similar to the spring spray (Table 2). The mortality in the acephate sprayed plot was 20% more than that in the methoxychlor sprayed one. The differences between acephate vs. methoxychlor and the sprayed vs. unsprayed are statistically significant ($P < 0.05$). The "negative mortality" in the unsprayed block may be due to an error in the prespray count. Possibly all the eggs may not have hatched yet, or larval cases may not have been large enough to be seen during counting. Also, *A. demotella* larvae may not have been present on the undersides of the leaves, as the *juglandis* larvae are, at this time. This phase of its life history is not yet well-defined.

Another type of bud damage was observed during the follow-up to the spring spray tests. This was frost damage. Frost-killed buds were counted when infested buds were tallied. In each treatment, except the unsprayed block of the single bud spray, frost caused a greater percentage of the bud injury than did *Acrobasis* spp. larvae (Table 3). Nearly 100% of the buds on the trees in the whole tree spray area were injured by the combination of *Acrobasis* larvae and frost. Frost was much less damaging in the areas where the single bud spray test was conducted. Areas are not adjacent, which indicates that the differences in frost damage are due to variations in microclimate such as greater cold air collection in lower areas.

The incidence of frost damage is greater in sprayed plots than in unsprayed (Table 3). This could be synergistic effect of the spray, but, since the combined injury is not consistently greater in sprayed plots, probably not. Many buds may have been infested by *Acrobasis* larvae first and later damaged by frost. Since it was not possible to determine definitely if frost or the insect had killed it, any bud which had frass and silk on or in it was counted as infested. Therefore, actual frost injury may be reasonably consistent, but seems to be lower in unsprayed plots where more buds were counted as infested.

The total percentage of injured buds remains at a relatively constant high level regardless of insecticide use. Because of this, a pruning technique was implemented to correct the forking of main branches after the terminal bud is killed, instead of trying to prevent it. Methods and results from a test of this cultural method follow.

MATERIALS AND METHODS (Cultural)

The pruning technique tested was not the usual procedure of removing the lower branches as the tree grows. This technique was designed to eliminate a fork in a branch the same year it forms. Only forks developing as a result of the terminal bud being killed (presumably by Acrobasis larvae or frost) were included.

Three treatments on approximately 50 trees each were employed. A terminal branch with 2 new shoots of approximately equal length and diameter near the tip were designated. On the 50 untreated trees these branches were simply numbered and labelled. For the first treatment, one of the 2 green shoots was removed and any other shoots further down the branch were left intact. For the second, all but one of the new shoots growing on the previous year's growth were removed so only one shoot forming the fork remained (Figure 5). These three treatments were executed randomly on 150 trees. The pruning was done in early June with a clean, sharp knife.

Table 1.--Efficacy data for spring spray of acephate and methoxychlor, Quincy, Michigan 1977

Treatment	Postspray[1]	Difference (Unsprayed-Sprayed)[2]
Single buds treated		
Acephate (n=54)	20% ± 0.7	34%
Methoxychlor (n=56)	30% ± 0.8	24%
Unsprayed (n=56)	54% ± 0.9	--
Whole tree treated		
Acephate (n=53)	10.0% ± 2.7	24.9%
Methoxychlor (n=48)	21.4% ± 3.1	13.5%
Unsprayed (n=52)	34.9% ± 4.7	--

[1] Mean ± standard error (percentage of terminal buds or shoots injured by Acrobasis).

[2] All differences between sprayed and unsprayed plots were significant (Students' t test, $P < 0.05$).

Table 2.--Efficacy data for fall spray of acephate and methoxychlor, Quincy, Michigan 1977

Treatment	Prespray[1]	Postspray[1]	Percent mortality[2]
Whole tree treated			
Acephate (n=50)	1.2 ± 0.2	0.3 ± 0.0	80.2% ± 9.2
Methoxychlor (n=49)	1.0 ± 0.1	0.4 ± 0.1	61.8% ± 18.1
Unsprayed (n=50)	0.7 ± 0.1	0.8 ± 0.1	-10.0% ± 32.8

[1] Mean ± standard error (number of Acrobasis larvae per terminal bud plus 15 cm of the branch).

[2] Mortality ± 95% confidence interval.

Table 3.--Comparison of Acrobasis injury to frost injury on black walnut (from postspray counts for spring spray test), Quincy, Michigan 1977

Treatment	Percent injured buds[1]		
	Acrobasis spp.	Frost	Combined
Single bud treated			
Acephate (n=54)	20% ± 0.7	52% ± 0.9	72% ± 0.8
Methoxychlor (n=56)	30% ± 0.8	55% ± 0.9	85% ± 0.6
Unsprayed (n=56)	54% ± 0.9	29% ± 0.8	83% ± 0.7
Whole tree treated			
Acephate (n=53)	10.0% ± 2.7	88.1% ± 3.2	100.0% ± 0.0
Methoxychlor (n=48)	21.4% ± 3.1	77.5% ± 4.9	95.1% ± 2.5
Unsprayed (n=52)	34.9% ± 4.7	63.6% ± 4.8	99.7% ± 0.2

[1] Mean ± standard error

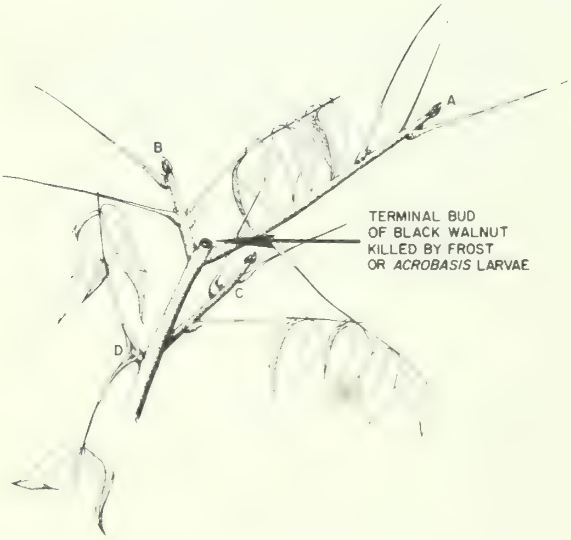

A
B
C
D
TERMINAL BUD OF BLACK WALNUT KILLED BY FROST OR *ACROBASIS* LARVAE

Figure 5.--Pruning techniques for correcting forking: 1) only B is removed, 2) B, C, and D are pruned and A becomes the terminal leader. Shoots were pruned in early June with a sharp knife.

In May of the following year, the pruning treatments were evaluated. A determination of whether the fork had been eliminated ("corrected" or not was made and measurements of the new (1977 and last year's (1976) growth on both treated and untreated branches were recorded. Healing of the branch where shoots had been removed, based on closure of the wound, was noted.

RESULTS AND DISCUSSION

This pruning technique appears to have corrected forking effectively. Forks were counted as "corrected" when only one shoot remained as the main leader and if the branch appeared to be nearly straight. On many of the branches where only one shoot was removed, another one further down the branch grew enough to form a fork comprised of it and the shoot left from the original 2 (Table 4). Removing all but one of the new shoots was effective in all instances.

The pruning of a single shoot resulted in a slight increase in growth compared to the untreated branches, but not enough to be statistically significant (Table 4). The treatment in which all but one shoot was removed did result in significantly greater growth. The ratios of 1977 growth to 1976 growth were used to compare the effects of each treatment on shoot growth. This was done to eliminate the bias towards faster growing trees in the second treatment.

Table 4.--Results of "corrective pruning" to reduce Acrobasis and frost injury on black walnut, Quincy, Michigan 1977

Treatment	Forking corrected?		Mean length in feet of branch growth[1]		Ratio[2]
	Yes	No	1977	1976	1977/1976
Single shoot removed (n=39)	62%	38%	0.7 ± .06	1.2 ± .09	0.6 ± .06
All shoots but one removed (n=34)	100%	0%	0.7 ± .06	1.2 ± .10	0.7 ± .09[2]
Untreated (no shoots removed) (n=45)	7%	93%	0.6 ± .04	1.2 ± .07	0.5 ± .04

[1] Mean ± standard error

[2] Significantly greater than untreated (Students' t test, $P < 0.05$)

Healing of the pruning wounds occurred very quickly. On the majority of branches, branch stubs were nearly healed over by the end of the growing season. Branches where all but one shoot was removed, healed faster than those where only one was removed. This may have been due to the increased growth of those branches.

SUMMARY

The results of this study suggest that acephate and methoxychlor are effective in reducing Acrobasis spp. damage and numbers. Either one may be sprayed in the early spring or early fall. Both chemicals are also effective when sprayed on single buds (spring test). This approach is more effective than whole tree spraying and can reduce spray and ime consumption. Acephate was 10 to 20% more ffective than methoxychlor in all three trials.

However, insecticides do not minimize frost damage which causes a major portion of he bud injury in some years. The pruning technique tested can correct forking caused y both frost and Acrobasis feeding, as well s increasing growth of the terminal shoots.

RECOMMENDATIONS

Our recommendation to walnut growers in Michigan is to correct forking of terminal branches by pruning rather than by applying insecticides. The new shoots developing along a branch may be removed, leaving one to become the terminal leader. This should be done in rly June when bud damage is apparent and fore shoot growth is completed. This treatment is only necessary on terminal branches in years when frost and insect damage is severe.

ACKNOWLEDGMENTS

Our sincere thanks to S. Wilson, J. Pasek, J. Nyrop, N. Krite, B. Kemp, and J. Ball for field assistance and to Mr. George Brown, owner of the black walnut plantation near Quincy, Michigan, for his cooperation. This work was supported in part by a grant from the U.S.D.A. Forest Service.

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GROUP DISCUSSION

Kuntz: Do you find any continued discoloration down the stem from the Acrobasis injury? Is there any associated dieback?

McKeague: We haven't found any.

Kuntz: Have you found any evidence of Melanconium fungus coming in on any of these injured twigs? Have you seen any sooty pustules or fruiting bodies?

McKeague: No, I haven't seen any evidence of disease.

L. Wilson: I haven't noticed anything with the butternut curculio either.

Schlesinger: Do you think that repeated single leader pruning on a tree which is continually attacked by *Acrobasis* will cause problems?

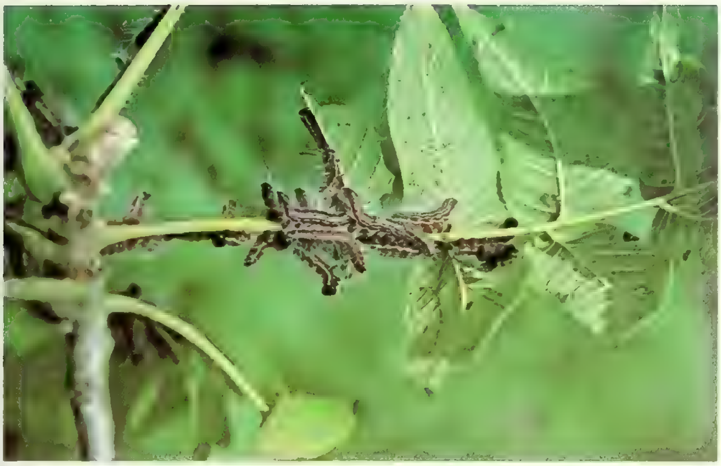
McKeague: If continual attack is a problem, I can't see that the repeated pruning would be a problem. We're not determining if there is only a single branch coming up. We're looking at the terminal leader. The lateral branches, of course, are not as crucial.

Schlesinger: No, I was just wondering if you would end up with a single leader if you pruned year after year. You are not allowing the laterals to develop on that growth.

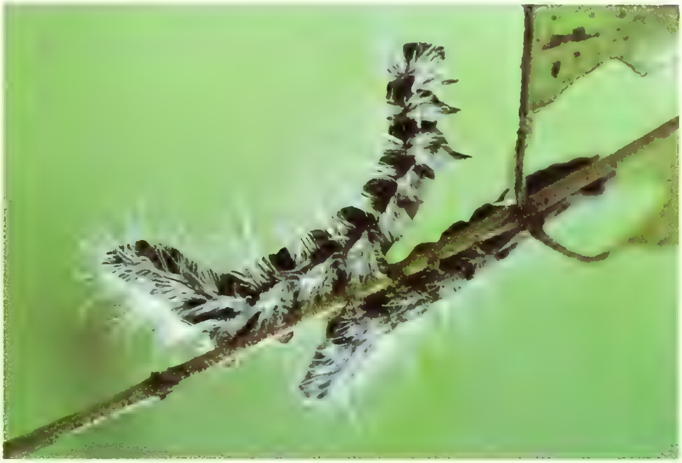
L. Wilson: This is probably an area where we might continue some research because it brings up a good point. What does happen to the trees? Perhaps this is something we can bring up tomorrow as a potential future study.

Shigo: In your abstract you state that "all but one of the new shoots of a damaged branch were removed in late summer," while in your presentation you said June. Can you clarify that?

McKeague: Yes. That was evidently a typing error. It should have said "early summer", since the branches were pruned in early June.

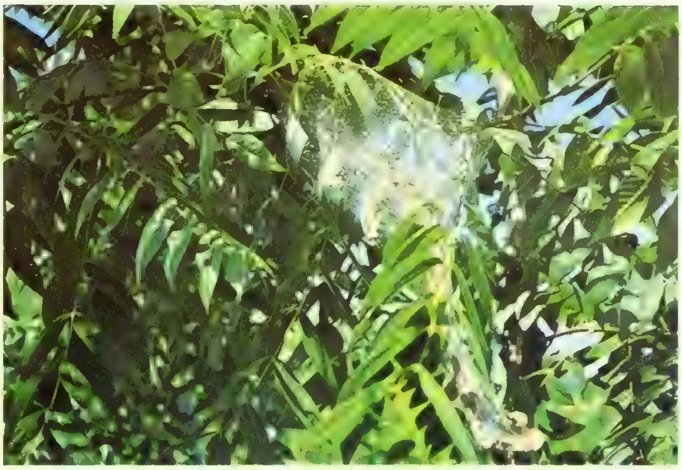


Feeding walnut caterpillars.

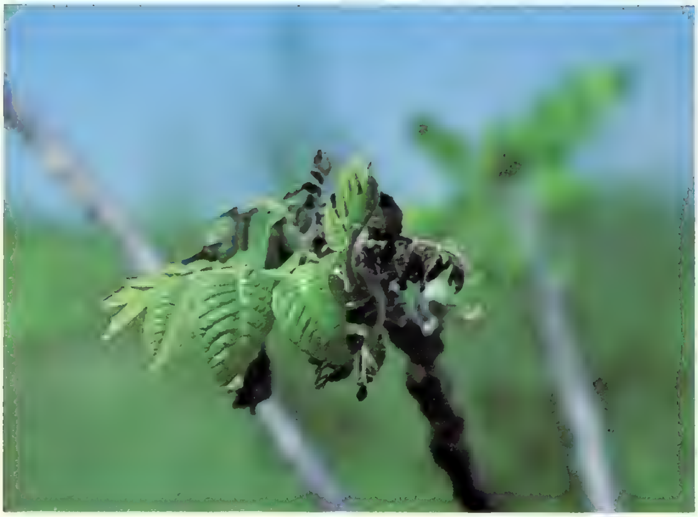


Walnut caterpillar 5th instar.

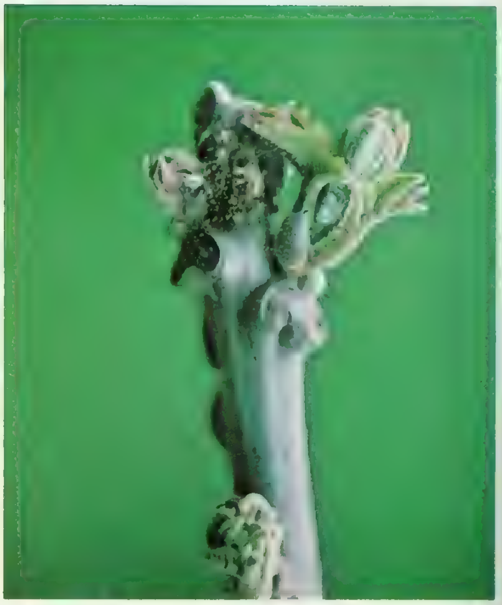
Walnut caterpillar defoliation.



Fall webworm.

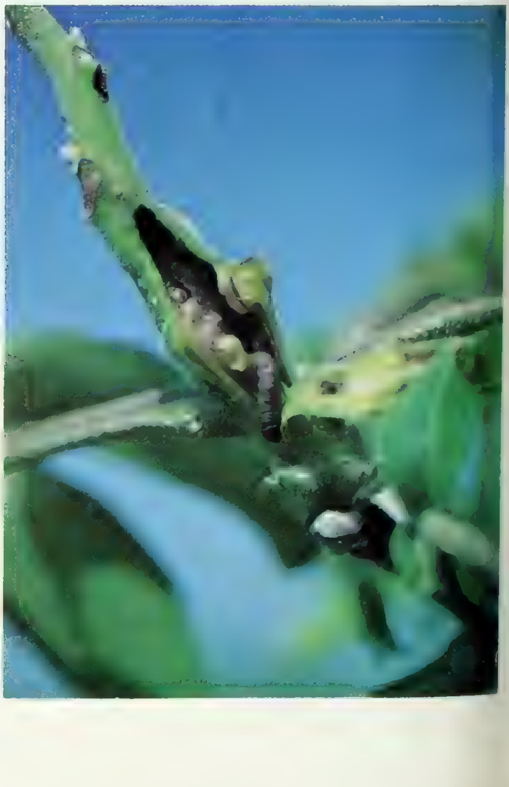


Dieback of young leaves due to *Acrobasis* attack.

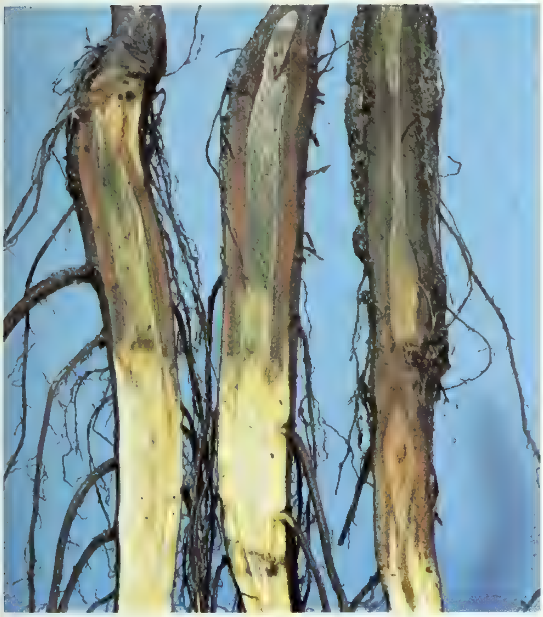


Frass typical of entrance by *Acrobasis* larva into newly expanding terminal bud. (Photo courtesy of W. H. Hoffard, S&PF, Asheville, NC.)

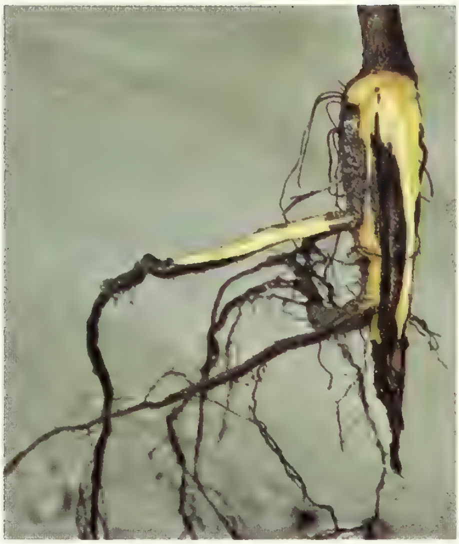
Tunneling larva of *Acrobasis demotella.*



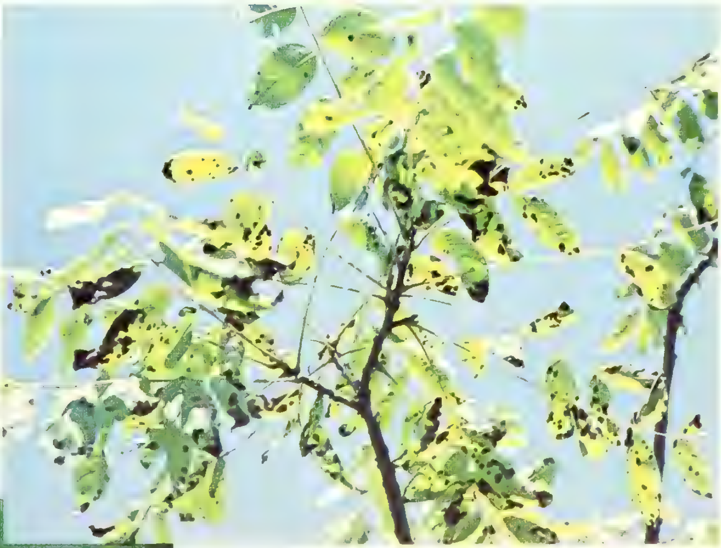
Oviposition injury to walnut fruit caused by walnut curculio.



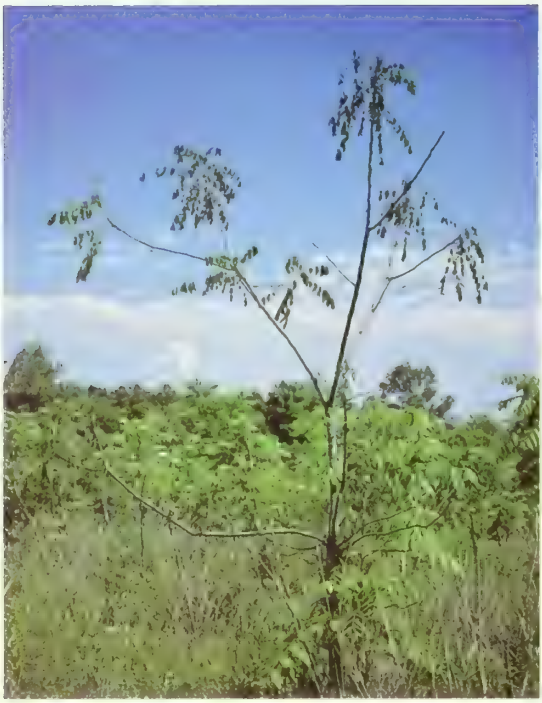
Phytophthora root rot.
(Photo courtesy of R. Green,
Purdue University.)



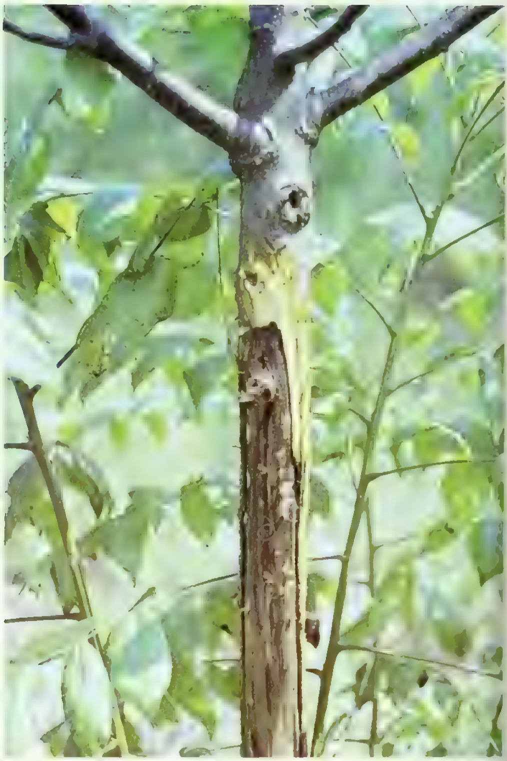
Cylindrocladium root rot.
(Photo courtesy of
D. A. Roth and G. J. Griffin,
VPI)



Anthracnose lesions on walnut
foliage and fruit.



Wilting foliage caused by stem girdling from a Fusarium canker.



Bark removed to show discoloration associated with Fusarium canker.

Butternut decline.

THE BLACK WALNUT CURCULIO AND ITS IMPACT ON NUT PRODUCTION

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Kansas State and Extension Forestry
Kansas State University
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and

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University of Missouri
Columbia, Missouri

ABSTRACT:--The black walnut curculio, Conotrachelus retentus (Say), is an important pest to black walnut nut production. Adult curculios feed on walnut foliage and oviposit on developing nuts in May and June. The infested nuts drop from trees before reaching maturity. Missouri nut productivity studies conducted in 1976-77 revealed curculio related losses of 78%, 66%, 43%, and 19% to nut crops in three geographic areas of the state. The black walnut curculio was found to be the major factor among four factors which influenced early nut drop in black walnut.

Expanded uses for black walnut nuts have added a new and potentially profitable aspect to walnut farming. Demand for nut products is steadily increasing, and management practices now recognize and support nut production as an economic plus for the species. Annual incomes from nut crops reduce the long-term carrying costs associated with plantation establishment and cultural operations. These costs are normally cancelled only when the trees are harvested at the end of the rotation.

Black walnut nuts are valuable both from he standpoint of regeneration and industry. ncreased landowner awareness of the value f walnut timber has caused a significant ncrease in demand for walnut seedlings. ost states have been unable to meet these emands because of nut scarcity (Grey 1973). his problem has been complicated by competition rom the nut industry. Aside from the importance f the walnut kernel as a food item, research as shown important uses for crushed shells. mong these are use as filter agents in smoke-ack scrubbers, additives to drilling mud in l well drilling, polishing agents for chrome d automotive parts, and many others (Cavender 73). Poor quality walnut kernels which were ce wasted are now ground and added to live-ock feed as a nutritional booster. Continued search promises additional uses for black lnut nuts in the future.

Insects which affect nut productivity must be considered an important component of black walnut management. The black walnut curculio, Conotrachelus retentus (Say), is an important pest. The adult feeds on new shoots and leaves, and the larva destroys the developing nut. Little information has been available on the habits of this pest. Therefore, a comprehensive study was conducted in 1976-77 to determine its life history and impact on nut production in Missouri.

LIFE HISTORY

The life cycle of the black walnut curculio encompasses about 13 months. Adult curculios overwinter in the soil or under organic litter on top of the soil. Spring emergence begins in mid-April and continues for several weeks. Newly emerged adults enter the nearest black walnut tree and feed on succulent foliage and staminate flowers. Feeding damage occurs primarily on the base of the leaf rachis, and appears as a small darkened area. This damage seldom causes leaf death, and is difficult to detect. Occasionally, the curculio chews holes in walnut leaflets, but this damage cannot be distinguished from that of other leaf-feeding beetles.

Oviposition begins on developing nuts shortly after the female flowers are fertilized. In young nuts, single eggs are placed in crescent shaped punctures chewed from the wall of the nut. More than one crescent may be present on a nut, and several eggs may hatch. However, the most vigorous larva will consume the others to insure an adequate food supply for its own development. On larger more mature nuts, single eggs are placed in ovipositional punctures which resemble pin holes. These punctures are usually placed on the nut in clusters of 3-10. It is not uncommon for several larvae to complete their development in large nuts with diameters of 3.8 cm or larger.

Rarely, black walnut curculios oviposit in elongating shoots of black walnut. The developing larva generally tunnels toward the terminal bud to remain in succulent tissue. Surveys of Missouri black walnut plantations under 10 years of age revealed no curculio activity in young trees. Adult curculios evidently do not associate with trees too young to bear nut crops. All oviposition is complete by the end of June.

The curculio larva hatches from the egg about 5 days after oviposition. The larva bores into the center of the nut and consumes its contents. The infested nut drops from the tree about 3 weeks after oviposition occurs. The larva remains inside the hollowed out nut for an additional 2 weeks before entering the soil to pupate. When fully grown, the larva is about 11 mm long. Duration of the larval stage is about 5 weeks.

The larva exits the nut by chewing through the nut wall. Exit holes are about 5 mm in diameter, and serve as evidence of curculio activity. After entering the soil, the larva forms a smooth-walled cell where it undergoes physiological changes for several days prior to pupation. The pupal stage occupies a period of about 3 weeks.

Summer adult emergence begins in mid-July and continues into August. These adults feed on black walnut foliage until leaf drop occurs. No reproduction takes place until the following spring.

IMPACT ON NUT CROPS

Missouri nut productivity studies were conducted in one area in 1976, and three areas in 1977. The initial study involved testing and comparison of three trapping variations at the Dupont black walnut plantation near Ashburn, Missouri. Trees in the plantation were 27 years old at the time of the study. Thirty-six trees were selected and sampled with 216 cone-shaped plastic traps (0.8 m diam). Each trap was suspended between two 5 foot stakes (132.4 cm). Trap placement was statistically designed to accurately estimate damage for the entire plantation from sample tree collections.

Traps were checked weekly from early June until August, and biweekly for the remainder of the season. The collected nuts were dissected to determine the reason for early drop. Records were kept for each nut. Four factors were determined to influence premature abortion and loss to nut crops. These included curculio damage, infertility, squirrel activity, and natural abortion in response to moisture stress. Curculio damage had the greatest impact of the four factors. It accounted for 88% of the premature drop recorded during the 2 years of productivity studies.

Seasonal nut drop at the Dupont plantation in 1976 occurred in two distinct periods (Figure 1). The "June nut drop" included all nuts which dropped before August 17 as a result of the four previously mentioned factors. These nuts were lost to production. The mature nut drop occurred from September 15 to November 5. Nuts which dropped during this period were harvestable. The black walnut curculio reduced the nut crop by 43% at Dupont in 1976.

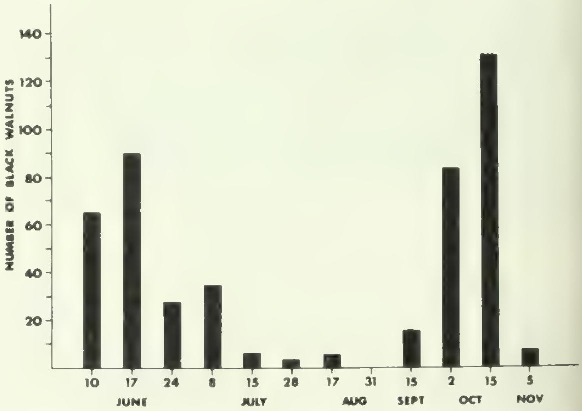


Figure 1.--Seasonal distribution of black walnu nut drop at the Dupont plantation, Ashburn, Missouri, in 1976.

The 1977 black walnut productivity study was expanded to include trapping sites in three geographic areas of the state. The Dupont plantation was again used to represent the northeastern part of Missouri. An unmanaged tract of black walnut near Fayette, Missouri was used as a central Missouri site. The third site was an intensively managed black walnut fertilizati plot in southwestern Missouri, near Stockton. Sample trees were of nut-bearing age, and range from 24 to 32 cm DBH. Thirty trees were random selected in each area. Each tree received four traps.

Seasonal nut drop at the Dupont plantation differed greatly in 1977 from that of the previous season (Figure 2). Only a small percentage of the nuts reached maturity. Disregarding other factors, curculio damage was responsible for a 78% reduction of the potentia harvestable yield.

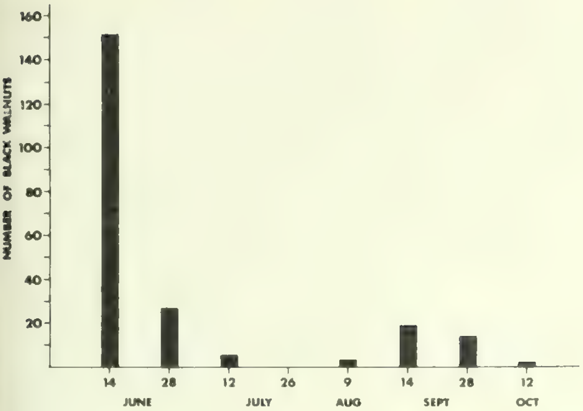
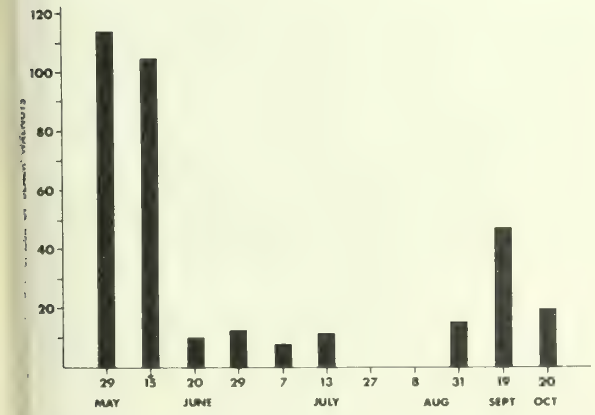


Figure 2.--Seasonal distribution of black walnut drop at the Dupont plantation, Ashburn, Missouri, in 1977.

A similar level of damage was recorded at the Fayette trapping site (Figure 3). Again, more nuts were collected during the June nut drop than during the mature drop. Sixty-six percent of the crop was destroyed by curculio activity.



igure 3.--Seasonal distribution of black walnut nut drop in natural forest, near Fayette, Missouri, in 1977.

The Stockton area was least affected by remature nut drop (Figure 4). Most of the rop reached maturity at this site. Curculio tivity destroyed only 19% of the developing ts. This level of damage was not consistent th other Missouri areas. The comparatively w impact was possibly linked with site sturbance effected by former practices in e stand. Activities which affected the site included annual applications of simazine and paraquat to remove grass under trees, bulldozer work to release single trees, and the use of heavy equipment in an intensive spray schedule involving foliar fertilizer. It is believed that the combination of compacted soil and lack of normal ground cover may have adversely influenced curculio populations on the site. This might explain the reduced level of curculio damage.

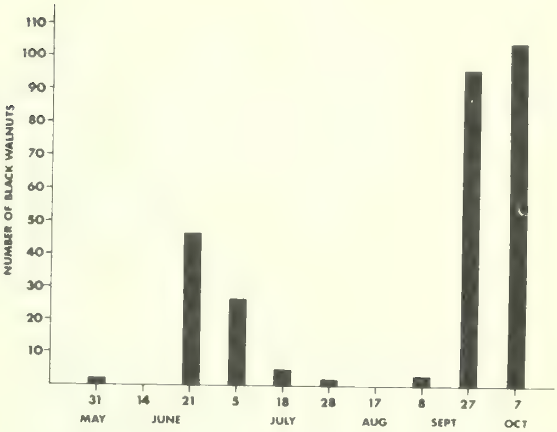


Figure 4.--Seasonal distribution of black walnut nut drop at the Fox plantation, Stockton, Missouri, in 1977.

CONCLUSIONS

Seasonal nut collections in 1976 and 1977 showed that the black walnut curculio had an important impact on black walnut nut production in Missouri. Statewide, 51% of the nuts collected in productivity studies dropped prematurely as a result of curculio activity. This indicates that control measures may be warranted where annual incomes from nut crops are desired. Continued research is needed in developing a sound control program to reduce the impact of this pest.

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GROUP DISCUSSION

Weber: One comment about what we are finding in southern Illinois. We do find Conotrachelus retentus weevil adult ovipositing in the newly developing leaflets in the spring. We find that eggs inside the petiole and some years there is a lot of that kind of damage in southern Illinois.

Blair: Well, that's real interesting. This type of damage could have some real economic ramifications in young plantations where these insects are mining out the terminal buds. Dr. Kearby and I rather extensively surveyed several plantations in Missouri and looked for this damage. In the laboratory I initiated a special study in which I introduced a number of mated pairs of weevils into cages containing walnut seedlings. There was no nut source in which to oviposit. I tried to force them to oviposit in the stems and I got only one instance of petiole oviposition in two years. I artificially inoculated some of the stems with eggs that I had collected and they hatched and developed normally. So we feel that it really is not a problem in Missouri. So I am glad to hear that it is a problem down here in this part of the country.

LaMadeleine: You said that you had some help in developing your statistical survey technique and that you had a phenomenal number of sampling bags there in the study area. Do you have a feeling for how many samples are necessary to determine impact on an area? How would you set up your system?

Blair: In the first study, we studied 6 trees and used either 4, 6, or 8 traps. We found that there was no statistical variation between the means collected in either 4, 6, or 8 traps. So, in our expanded program we used 4 traps per tree and found that we needed a minimum of 30 trees in an area to really mean anything to us. So we went with 30 trees to study weevil impact on the trees.

LaMadeleine: Then you used 30 trees, regardles of the size of the plantation?

Blair: Right. Our method was to go in and map the plantation, or mark the trees. If it was a native stand, our sample trees were then selected by means of a random numbers table. To further randomize the design, we marked off 8 sections beginning at due north and rotating through each 45 degrees in a clockwise direction around each tree and drew from a random numbers table to determine where the trap would go around that tree. It was a very complet job of statistics.

Weber: Have you reared out any other species of Conotrachelus?

Blair: I did. This was almost a fluke. I reared one Conotrachelus elegan which is the big nut curculio. I sent it to Lester Gibson in Ohio for positive identification and he wrote me a letter confirming the identification but also indicating surprise. The specimens were in containers where we were using sterilized soil and rearing anything that came out. I have found Conotrachelus elegans associated with black walnut nuts for quite some time and always thought that they might complete their development in the nut itself. They feed readily on the foliage and act very similar to Conotrachelus retentus in their life cycle.

Weber: The reason that I asked was that I have reared out Conotrachelus anaglypticus which is a pest on fruit trees.

THE LIFE HISTORY OF ACROBASIS DEMOTELLA AND ITS ROLE IN SEEDLING AND SAPLING STEM DEFORMITIES IN MISSOURI[1]

William H. Kearby

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University of Missouri
Columbia, Missouri

ABSTRACT.--The lepidopterous shoot borer, Acrobasis demotella Grote, is the most destructive borer in terminal shoots of black walnut seedlings and saplings in Missouri. The larvae overwinter in hibernacula and emerge at bud swell to feed on buds and tunnel in shoots. Larval activity occurs during April and May. The larvae exit the shoots and move to the soil to pupate. Adults emerge in June and lay eggs on the foliage. After eclosion the larvae feed on leaves prior to forming hibernacula near the axils or bases of new buds. It is univoltine.

The impact of this insect is stem deformities on 1 to 5 percent of the trees grown in plantations in North Missouri in most years.

In Missouri the black walnut tree affords the greatest opportunity for long-term economic gains when compared to other forest or plantation grown trees by providing nuts, shells, lumber, and veneer logs. Add to these the multicrop concept such as a cow-calf operation with grass, wheat or soybeans and a sustained economic operation is underway. However, with relation to geographic location and site factors, particularly soil, drainage, slope and elevation, several problems may occur annually when attempting to establish a new plantation. Annually black walnut seedlings and saplings have been damaged by flooding, frost, mammals, pathogens and insects. Kearby (1976) reported 2 species of insects feeding on various parts f black walnut trees during 1974 in Missouri. f these the bud and shoot feeding insects were he most important, since loss of terminal buds nd shoots on young trees adversely affects heir future form. This paper discusses only ne species, a pyralid, Acrobasis demotella rote.

SITE SELECTION

Two major vegetative geographic areas were examined in Missouri. The prairie, where black walnut grows along creeks and larger streams in Boone, Carroll, Clay and Macon Counties north of the Missouri River, and the oak-hickory forests of Cedar, Dade, Hickory and Texas Counties south of the river. The topography varies from level to rolling or hilly slopes.

SAMPLE UNITS

In plantations and natural stands, seedlings and saplings to a height of 3 meters were examined for various stages of Acrobasis demotella and damage. The sample units were terminal buds, terminal shoots, lateral buds, and lateral shoots. The terminal buds are those buds on the apical 3 cm of the terminal shoot. The terminal shoot is that shoot which assumes apical dominance during the form-phase of seasonal growth. The lateral buds are those buds on branch whorls 1 and 2 below the terminal shoot. The lateral shoots are new shoots that arise from whorls 1 and 2.

METHODS

The sample units were examined biweekly and weekly during the growing season and twice during the winter. The number of seedlings and saplings examined at each site varied with the size of the plantation or natural stand from 25 to 200 individuals. Those that showed previous shoot deformities were tagged and numbered for study. Trees that had no previous deformities were added to the study when overwintering hibernacula and early season shoot boring was observed at the eight sites. Terminal and lateral shoots were removed throughout the year and were examined in the laboratory for hibernacula and other immature stages of A. demotella. Infested shoots were used in rearing experiments in temperature controlled environmental chambers to observe development of the life stages.

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[1] Not presented at workshop.

BIOLOGY

Acrobasis demotella 1st and 2nd instar larvae overwinter in hibernacula located on the terminal buds or in the axils of lateral buds (Figure 1). The hibernacula range in length 1.1-1.5 mm and 0.8-0.9 mm in width. They are downy and gray and blend well with buds of black walnut. The larvae emerge from the hibernacula at bud swell and feed on the expanding buds. As shoot elongation occurs, a larva will bore into the axil where the leaf petiole attaches to the shoot. The larva tunnels downward into the pith 2 to 5 cm. The presence of a larva in an elongating shoot is noted by a small amount of loose frass and silk near the entrance hole. Larval feeding in shoots occurs in April and May. Most larvae complete feeding by late April. The last stage larva is 14 to 17 mm long, head reddish brown or dark brown and the body is purplish with green undertones (Neunzig 1972). The larva leaves through the enlarged entry hole in the shoot and moves to the soil. Pupation occurs just beneath the soil surface in a thin cocoon surrounded with soil particles. In the field moths emerged the last week of May through mid-June. In the laboratory fertile females laid single eggs on leaflets of caged seedlings. A few larvae hatched and fed lightly on the undersurface of the leaves. Within a week the 1st or 2nd stage larvae moved to the stem and spun hibernacula. In the field hibernacula were observed on buds in August. It has a single generation each year.

DAMAGE

Black walnut saplings on poor sites are adversely affected by A. demotella larvae feeding on small terminal bud clusters. The larvae may destroy the entire cluster or only the terminal bud prior to expansion of the shoot. This feeding causes a blunt shoot or a forked top. The injury is similar to a very early frost but is not uniform throughout the stand.

Last stage larvae usually leave the shoots prior to any noticeable shoot symptoms. Wilted shoots with necrotic leaflets occur above the larval tunnel in late May and early June (Figure 2). Damage by A. demotella can be separated from April frost damage by the tunnelled pith contrasted to shriveled hardened pith. Insect damage is scattered throughout a stand whereas frost damage is uniform on adjoining trees or the entire stand. Tunnelled shoots dry and break and leave a blunt stub or a portion of the hollowed shoot intact (Figure 3).

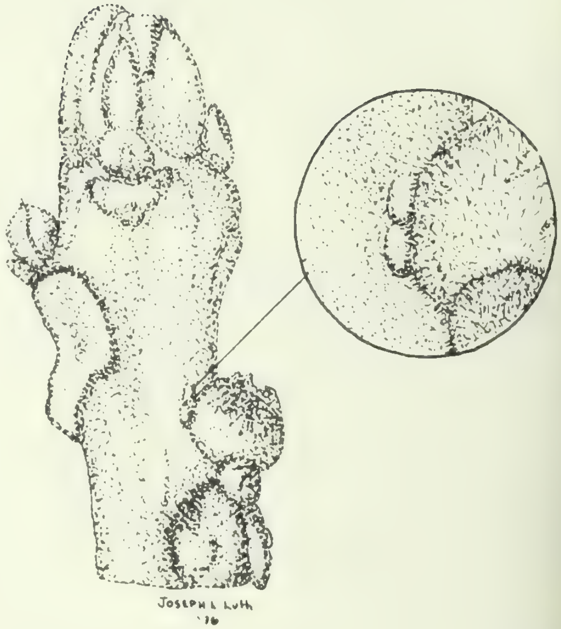

Figure 1.--Diagrammatic illustration of a black walnut terminal showing the location of the hibernacula.

CONCLUSION

In north Missouri on the best black walnut sites A. demotella is one of the major causes of stem deformities. However, other insects particularly scarab beetles, cause early bud loss (Kearby 1976). The total shoot loss in a plantation may range from 1 to 5 percent a year. This varies with sapling size and the same trees are not re-infested in successive years. Therefore, shoot damage becomes compounded over a 5-year period. Trees that expand rapidly in the spring are less susceptible to bud and shoot injuries caused by A. demotella and other insects. Only the better sites should be selected for planting to prevent excessive insect deformities.

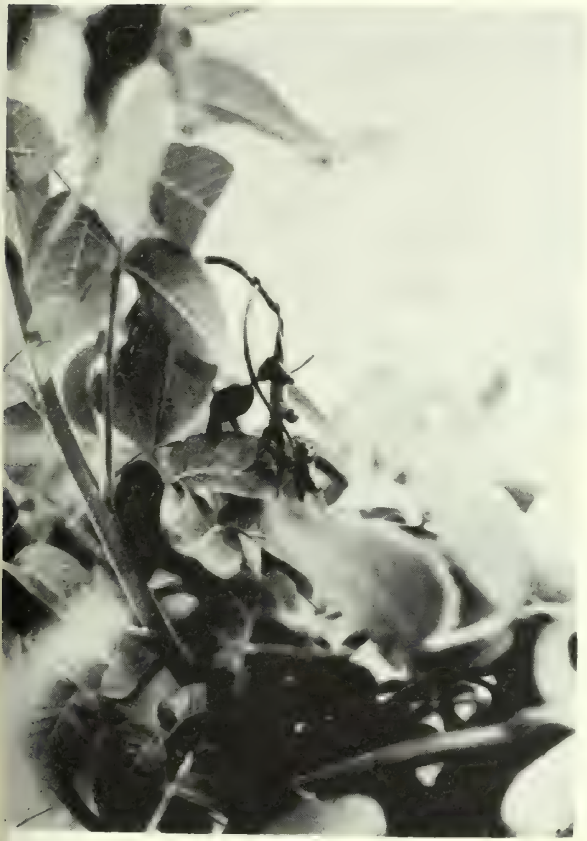

Figure 2.--*Terminal shoot mortality caused by the larva of A. demotella.*

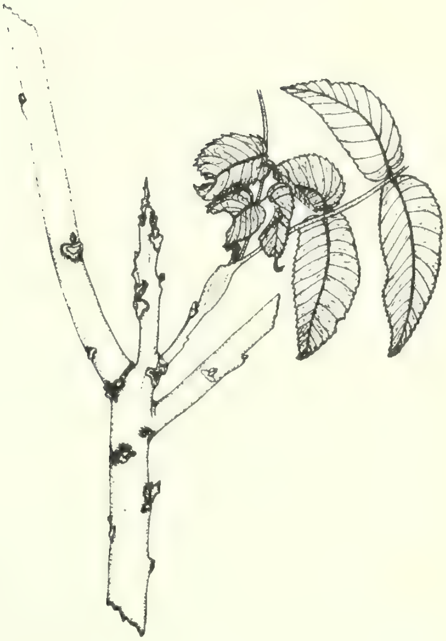

Figure 3.--Diagrammatic illustration of a tunnelled black walnut terminal after the tip has broken off in midsummer.

LITERATURE CITED

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ETIOLOGY, EPIDEMIOLOGY AND CONTROL OF BLACK WALNUT ANTHRACNOSE

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ABSTRACT.--Walnut anthracnose, caused by Gnomonia leptostyla, is the most serious and widespread foliar disease of black walnut. Literature on the causal agent and etiology and control of the disease is limited. In Illinois studies, we have isolated the causal fungus from trees from several states and compared the cultural characteristics, growth rates, sporulation, and spore germination of the isolates with several media, temperature, pH, and light variables. The presence of heterothallism was confirmed. We have artificially inoculated black walnut seedlings (and mature plants) with varying inoculum concentrations and observed lesion initiation and development. Leaf rachises are the apparent overwintering site for the fungus and ascospores are the primary inoculum in the spring. Free water on the leaf surface for 6 to 24 hours is essential for infection. Conidia in acervuli are produced after 2 to 3 weeks and serve as the inoculum source for secondary and repeating infections. Lower light intensities favored disease severity. Species and hybrids of Juglans varied in resistance to Gnomonia leptostyla. Partial control of disease in the field can be obtained through fertilization with nitrogen fertilizers and application of protective fungicides (especially benomyl) during the last week of May and the first week of July.

Walnut anthracnose, caused by Gnomonia leptostyla (imperfect stage--Marssonina juglandis), is the most serious and widespread foliar disease of black walnut. Literature on the causal agent and etiology and control of the disease is limited. Only three individuals have conducted extensive research on Marssonina juglandis: H. Klebahn in Germany in the early 1900's, F. H. Berry in Maryland in the 1950's, and J. Fayret in France in the 1960's and 70's.

Klebahn recognized the disease on black walnut. He described the symptoms and the asexual fruiting bodies of the fungus on the leaf surface. He also isolated the causal fungus to pure culture and established its pathogenicity with infection experiments. In addition, he described the fungus in agar culture and observed both macroconidia and microconidia. Klebahn obtained perithecia from overwintered leaves and studied and described the perfect stage of the fungus.

Berry was interested in the etiology and control of the disease. He collected perithecia from overwintered leaves and observed the discharge of ascospores, the primary inoculum, in the spring. He also observed the occurrence on leaflets of acervuli and conidia, the inoculum for secondary infection, and associated their dissemination with rainfall. He found few overwintering sites other than the peritheci on fallen leaves. Berry was able to artificiall inoculate plants successfully and related infection with rainfall. He observed anthracnose infections on 40 varieties of black walnut and applied foliar sprays and ground sprays of fungicides in control studies.

Fayret reported on the mycology of Gnomonia leptostyla. He found that perithecial production was favored at temperatures between 7° and 10° C and was slightly reduced by light. He reported that as photo-inhibition of sexual morphogenesis progresses, photo-induced conidiogenesis increases. Acervulus production was greatest at 18° C, and microconidia were produced at 10° C. He established that the union of two complementary mating types (heterothallism) is required for perithecial production.

In our studies in Illinois, we have obtaine additional information on (1) the severity of th disease on black walnut and its effects on the host plant, (2) the factors influencing growth and sporulation of the causal fungus and germination of the spores, (3) the microenvironmental variables regulating the inoculum at the infection site, (4) the climatic factors governing epidemiology in the field, (5) the resistance to disease within the genus Juglans, and (6) the cultural practices that control or reduce the effects of the disease.

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[1] I wish to acknowledge the contributions of William M. Black and James A. Matteoni, who while graduate research assistants at the University of Illinois, contributed substantially to our better understanding of this disease.

SEVERITY

In a five-state, 1200-mile survey in 1975, we examined roadside black walnut trees and collected diseased leaf specimens for examination and isolation. G. leptostyla was the predominant cause of leaf lesions. Microstroma juglandis and Cristulariella pyramidalis were two additional fungus pathogens found on walnut, but the major causes of premature leaf yellowing and defoliation, other than anthracnose, are noninfectious agents.

MYCOLOGY

The growth of G. leptostyla on all laboratory culture media was slow with more than three weeks' incubation required for the fungus to form a 9.0-cm wide colony. Oatmeal agar was the most favorable medium for vegetative growth and asexual sporulation of the fungus.

The fungus grows on culture media with an initial pH ranging from 4.5 to 10, but grows best on media with pH 5.0 to 7.0. Vegetative growth and sexual sporulation are favored at the lower pH, with asexual sporulation favored at the higher pH. Leaf pH may be one of the factors determining the change from the production of the conidial stage on attached leaves to the microconidial and perithecial stages on the more acidic fallen leaves.

The fungus is adapted to moderate temperature. An incubation temperature of 22° C was optimum for vegetative growth, and 26° C was optimum for asexual sporulation. The sexual stage is formed in response to cooler temperatures, 6° to 10° C. No growth was observed in vitro at 30° C.

Light favored asexual sporulation but educed vegetative growth. The development of he sexual stage was favored by darkness, which ould prevail in the decaying host material in eaf litter.

Provenance studies of fungus isolates ndicated only random, limited variation in rowth, germination, and sporulation of fungal ultures from several states.

Germination of spores taken from isolates aintained in pure cultures or obtained directly rom infected leaves occurred rapidly. While n significant germination of ascospores took lace within 6 hours, within 12 hours 40% germination occurred at temperatures ranging from 1° to 30° C, with optimum germination at 26° C Nine hours were required for significant conidial germination. Optimum temperatures were 22° to 26° C. Neither germination in culture nor infection of leaves was observed with microconidia exposed to favorable temperature, moisture, and nutrient conditions.

The presence of heterothallism was confirmed. All self-crosses were sterile. Colony types producing either protoperithecia or black perithecium-like structures, as described by Fayret, were observed, and crosses between isolates with different colony types produced perithecia with mature ascospores.

PATHOGENESIS

Two artificial inoculation procedures were employed. To provide moist environments, either a leaflet was enclosed in a plastic petri dish (Latham method), or several leaves were enclosed in a plastic bag that was gathered and tied around the plant stem. After a brief post-inoculation period, the humidity chamber was removed. Disease symptoms were abundant within 14 to 21 days under optimum conditions.

The study on inoculum concentration revealed that 100,000 conidia/ml gave the greatest number of lesions per leaflet, but that lesions developed from inoculum concentrations as low as 10 conidia/ml. With decreasing duration of free moisture on the leaf during the post-inoculation period, there was decreasing effectiveness of the inoculum. Under optimum laboratory conditions there was a logarithmic increase of infection frequency from 6 to 12 hours into the post-inoculation period.

In other infection experiments, the source of inoculum seemed to be of no special consequence: inoculum obtained from laboratory cultures or taken from lesions on affected trees seemed equally pathogenic. Substantial variability occurred in host plant susceptibility, however.

No differences in lesion character resulted from upper and lower leaf surface inoculations, but there was a great difference in infection frequencies. Nearly 10 times as many lesions resulted from placing the conidia on the lower surface.

The age of the leaf was related to disease susceptibility. Walnut is indeterminate in growth habits, and the immature, expanding leaves were not as likely to become infected as were the fully expanded leaves. In greenhouse tests using five distal leaves, all exhibited some lesions, but the lesions were smaller than normal on the three younger leaves and acervuli did not form on the two youngest ones. Lesions were large and acervuli abundant on the two older leaves.

Observations of fungal penetration were inconclusive. Scanning electron microscope studies indicated direct penetration through the cuticle and epidermis, with appressoria and penetration pegs. Penetration may also occur through glandular hairs. Stomatal penetration was not observed although it remains a possibility.

EPIDEMIOLOGY

Experiments related to the severity of walnut anthracnose were performed on seedlings in the greenhouse, in controlled-environment chambers, and on young trees in the field. When artificial inoculations were required, spore suspensions (5 x 10^4 conidia/ml) were brushed onto the upper and lower surfaces of the leaves (1 ml/leaf), which were then enclosed in a plastic bag, usually for 48 hours.

Attempts to isolate the pathogen from overwintering tissue proved difficult, since abscised leaflets decay rapidly. In one collection from Carbondale, however, 50% of the leaflets contained G. leptostyla perithecia. Pure cultures were obtained from these perithecia. Rachises of the compound leaf are very likely to overwinter intact. Seven percent of the rachises from Urbana collections contained perithecia, as did 25% of those from Carbondale. Perithecial production on dormant woody twigs was very limited, only three perithecia on bud scars on 200 twigs.

Spore trapping in Urbana confirmed previous observations that ascospores constitute the primary and conidia the secondary inoculum sources. Ascospores were trapped primarily between May 15 and June 5. Conidia were trapped after June 1, with the greatest number recorded between July 1 and July 31. A high correlation existed between total spores trapped and days with measurable rainfall.

Laboratory simulation verified the importance of precipitation for conidial dispersal. Wind alone or wind-blown wet leaves did not liberate spores from acervuli on infected leaves. Simulated rainfall onto wind-blown leaves, however, resulted in great numbers of liberated conidia.

Conidia on leaves abscised for 2 weeks or 1 month were just as virulent as mature conidia from lesions on leaflets still in the tree crown.

The effect of temperature on infection and disease development was investigated in controlled-environment chambers. Incubation of artificially inoculated plants at 21° C resulted in the maximum infection, while at 15° C significantly fewer lesions were evident. At temperatures of 10° C and below and 27° C and above, few lesions resulted. When plants incubated at 10° and 15° C were transferred to 21° C chambers, latent infections became evident. This phenomenon was not observed on plants originally incubated at 27° or 32° C.

Free moisture on the leaf surface is essential for infection. At 32° C during the post-inoculation period, only 1% to 3% infection occurred no matter how long free moisture remained on the leaf surface. At 21° C, as time with free moisture increased from 6 to 24 hours, the proportion of leaflets that became symptomatic increased from 3% to 90%. At 10° C post-inoculation temperature, significant increases were noted as time increased up to 48 hours.

Free moisture need not be present at the time the inoculum comes to rest on the leaflet surface. The inoculum retained infectivity on dry leaves for up to 2 weeks, and upon wetting of the leaf, lesions resulted. The longer the dry period, the fewer the lesions.

The anthracnose pathogen was capable of infecting susceptible tissue only within a narrow range of relative humidity (98% to 100%). High relative humidity promotes infection primarily through the prolongation of the time that free moisture remains on the leaflet surface.

Light intensity also had a significant effect on walnut anthracnose severity. Shaded seedling plants had from 80% to 90% of the foliage infected. Plants under clear glass had 13% of the foliage affected, and plants in full sunlight had 8% of the foliage affected.

A period of darkness during the first hours of the post-inoculation period resulted in an increase in the percentage of inoculated leaflets infected. Forty-eight hours of continuous darkness or of dark/light in a 12-hour cycle gave significantly more infections than did continuous light or light/dark in a 12-hour cycle.

Seedlings growing slowly in a heavy soil potting mixture in the greenhouse were more susceptible to anthracnose than were their vigorous counterparts growing in a fertilized peat:sand potting mixture.

The availability of soil moisture at the time of inoculation (within 48 hours), varying from 50% to 100%, did not appear to affect susceptibility to the anthracnose pathogen. When these moisture levels were maintained throughout the incubation period (2 weeks), the drier plants exhibited fewer lesions.

RESISTANCE

Artificial inoculation of various nut trees revealed a wide variation in host resistance to Gnomonia leptostyla infections. Leaf lesions developed on walnut, butternut, and heartnut, but no infection was evident on chestnut, hickory, or pecan. Arizona walnut and black walnut were very susceptible, whereas the clones of English walnut varied from very susceptible to resistant. Japanese walnut was the most resistant.

Hybrids from crosses between species of Juglans also were variable in resistance. Black walnut x Hinds walnut hybrids exhibited more lesions than did black walnut alone. Black walnut x J. microcarpa hybrids also were quite susceptible. English x black walnut hybrids varied from susceptible to resistant. Black walnut x Japanese walnut hybrids were most resistant.

The progeny from 57 parent trees were rated for anthracnose resistance in southern Illinois. Selected families which exhibited high incidence of anthracnose in 1974 also were severely infected in 1975 and 1977. The anthracnose rating system seems consistent enough from year to year to make genetic selection for anthracnose effective. Correlation coefficients for height, diameter, and anthracnose ratings were mostly not significant, suggesting that separate genes affect growth and anthracnose resistance. Our results indicate that anthracnose-resistant families are not necessarily rapid growing, but the faster growing families tend to be more resistant.

FERTILIZATION

Supplementing the soil nutrients with N and NPK significantly stimulated the growth f young black walnut trees in plantations. urface applications at the rate of 6 pounds of /1000 square feet increased tree height by 2% over that of untreated trees. Fertilization ith N and NPK also affected anthracnose ratings: trees treated with nitrogen alone had substanially less anthracnose than trees that had been reated with NPK or those receiving no treatment. he effects were most evident during the early ortion of the growing season.

CONTROL BY FUNGICIDES

Between 1973 and 1976, eight commercially available fungicides were applied to established black walnut plantations or to trees in natural stands. In seven of eight tests, benomyl (Benlate, DuPont) was more effective than other materials tested. Since anthracnose infections can originate at any time between May 15 and October 15, the timing of fungicide sprays presents a problem. Four sprays at 3-week intervals starting May 15 gave excellent control. The use of two sprays, with the first applied in the last week of May to inhibit the primary infection by ascospores and the second applied in the first week of July to inhibit secondary infection by conidia, appears to be a practical alternative.

From 1973 through 1977 walnut anthracnose probably received more attention than did any other foliar disease of a deciduous tree species. We have carefully defined the variability of the causal agent and the environmental factors that regulate its growth and reproductive potentials. We can describe more fully the conditions that influence infection of the host by the pathogen and know how the environment regulates the general course of epidemiology. Control of the disease with protective fungicides is possible.

Still, we have much to learn before we can satisfactorily answer inquiries from the layman concerning disease control. We do not know how damaging the disease is to plant growth or nut production. We hesitate to recommend protective fungicide applications and/or the addition of fertilizers to mature trees when we do not know the risk-benefit ratio and whether the treatments are economically feasible. I am pleased that a plant pathologist has been transferred to the Carbondale laboratory and that a substantial portion of his time will be spent on research on this disease. Additional knowledge is needed and can be justified.

GROUP DISCUSSION

Payne: You said you don't know the effects of nitrogen on trees. Well, walnut trees can't fix nitrogen, so when they're producing a nut crop there is a total nitrogen drain all the time. You mean you don't recommend yearly application?

Neely: No, no, no. By that I was referring to nitrogen and its relationship to walnut anthracnose. Not the relationship between nitrogen and tree growth.

Smythe: Can you tie the variability of resistance of English walnut to some known factor such as site or seed source?

Neely: No, I am afraid not. We just haven't done enough work in this area. We do feel that our inoculation technique and our method of taking readings on infected trees are sufficiently good to use to obtain that kind of information.

Green: Do you get lesions on the current season's shoot growth as well as on the leaf lamina?

Neely: Unlike oak and sycamore anthracnose we have not been able to find such shoot lesions on walnut in Illinois. Others have described this on walnut, however.

XYLOSANDRUS GERMANUS (BLANDF.) (COLEOPTERA: SCOLYTIDAE), A NEW PEST OF BLACK WALNUT: A REVIEW OF ITS DISTRIBUTION, HOST PLANTS, AND ENVIRONMENTAL CONDITIONS OF ATTACK

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ABSTRACT.--In southern Illinois Xylosandrus germanus has recently been reported attacking black walnut, Juglans nigra L., that were infected with a Fusarium canker. X. germanus was introduced to the United States from Japan in 1932. It now occurs throughout S.E. Asia, Germany, and the northeastern United States and has a worldwide host plant range of 34 different genera. X. germanus is capable of attacking live trees under certain ecological conditions and also of transmitting disease.

The ambrosia beetle, Xylosandrus germanus (Blandf.) (Coleoptera: Scolytidae), is a recently discovered pest of black walnut (Kessler 1974). It was found on black walnut in association with stem-girdling cankers, caused by Fusarium spp., in a 6- to 7-year old walnut plantation in southern Illinois. Tree damage included cankers, top dieback, and resprouting from the base (fig. 1). Kessler (1974) speculated that the dieback problem in black walnut was due to a disease/insect association between two species of Fusarium (F. lateritium Nees and F. oxysporum Schlecht.) and X. germanus. Since then, I have found the mbrosia beetle/Fusarium complex causing simiar damage to young black walnut plantations n Indiana and North Carolina.

DISTRIBUTION

X. germanus was introduced to the U.S. from Japan. It was first described by Walter . H. Blandford (1894) as Xyleborus germanus. Reitter (1913) transferred germanus to the newly established genus, Xylosandrus. There are now 24 described species of Xylosandrus in the world, including 3 introduced species in the United States: X. compactus (Eichh.), X. zimmermani (Hopkins), and X. germanus (Bright 1968).

X. germanus occurs throughout Japan, China, Korea, Formosa, and Germany (Wichmann 1955a). X. germanus was first reported in the United States in 1932 on greenhouse-grown grapes (Felt 1932) and is now distributed throughout the Northeastern United States (fig. 2) (Bright 1968, Schneider and Farrier 1969, Kessler 1974).

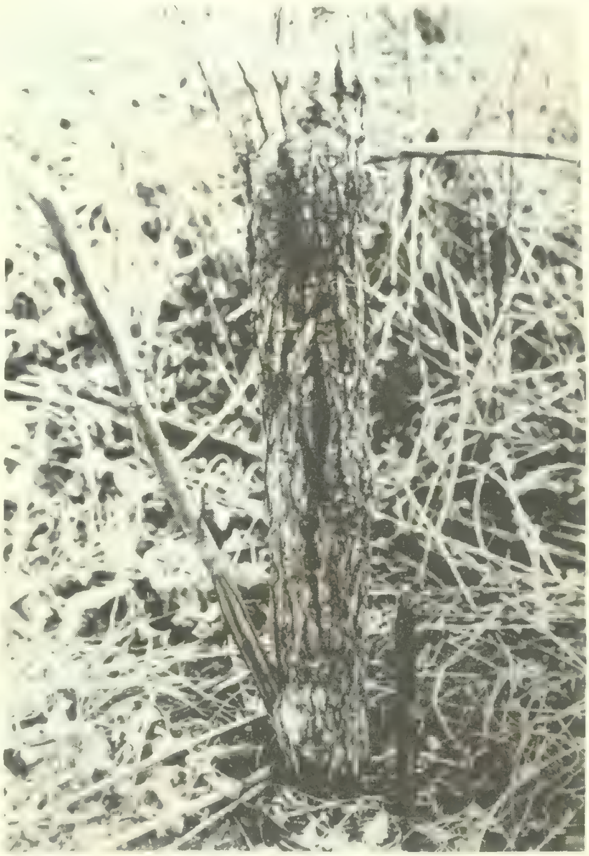

Figure 1.--Basal trunk sprouts and canker typical of attack by the X. germanus/Fusarium complex. Photo courtesy of Charles E. Cordell, State and Private Forestry, Asheville, North Carolina.

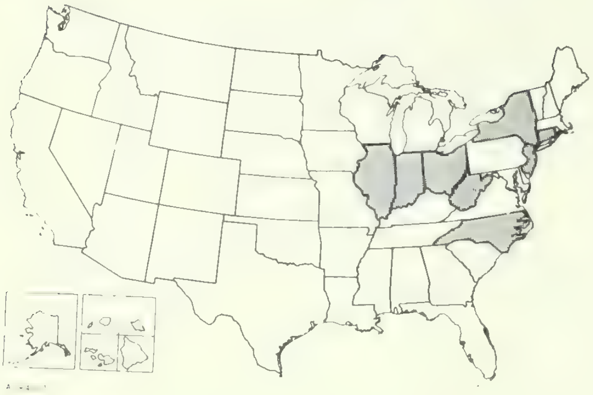

Figure 2.--Range of X. germanus within the continental United States.

HOST PLANTS

X. germanus has host plants in 34 genera throughout its worldwide distribution (table 1). In Germany, Wichmann (1955b) reported Juglans regia L. as a questionable host because no beetles were found. The galleries found in the wood, however, were characteristic of the X. germanus galleries found in other species of trees.

In the United States most species of ambrosia beetles attack woody stumps, logs, wind-broken branches, and dead standing trees. However, in Japan and Germany, as well as in the United States, X. germanus has been reported attacking live trees: red maple, elm, and young black walnut trees in the United States (Hoffmann 1941, Kessler 1974), young red oak trees in Germany (Heidenreich 1960, 1964), and tea bushes in Japan where X. germanus is considered a serious economic pest (Kaneko et al. 1965).

RELATION TO DISEASE-CAUSING ORGANISMS

As well as attacking trees, X. germanus is a disease carrier. Ceratocystis ulmi (Buis.) Moreau, the causal agent of Dutch elm disease, has been found on X. germanus (Collins 1941, Jones and Moses 1943, Batra 1963) and beetles have been proven to transmit it to healthy elm trees (Buchanan 1940, 1941). Also, Kessler (1974) suggested that beetles may carry Fusarium fungi to live walnut from nearby dead wood. In Germany Gauss (1960) noted that dead and dying trees of Acer pseudoplatanus L. had been attacked by X. germanus. At the same time, he noted the presence of Fusarium spp. and Phomopsis spp. The decay fungi, Schizophyllum commune Fr. and Polypora fomentarius (= Fomes fomentarius L. ex Fr.?), have also been found in trees attacked by X. germanus (Heidenreich 1964). No disease association has been reported in Japan.

X. germanus has two small pouches (mycangia), which are formed by the integumental membrane between the first and second segments of the thorax (Francke-Grosmann 1956, 1963, Takagi and Kaneko 1965). These pouches contain the spores of the fungus on which the beetles (adults and larvae) feed. This fungus may also be a disease-causing agent.

The X. germanus female tunnels into the wood, constructs a brood gallery, and lines the walls of the gallery with spores. Then, she carefully tends the developing fungi which is the food for the larvae when they hatch to prevent overgrowth by contamination from undesirable fungi. Eventually, new spores are produced. Movements by the offspring cause their pouches to fill with spores with which to line their own galleries. According to Batra (1967), the primary fungal symbiont of X. germanus is Ambrosiella hartigii Batra, a nondisease-causing fungus. At times, however, spores of other fungi may be picked up and deposited in the mycangia (Batra 1963). Interestingly, the fungal symbiont of X. compactus (Eichh.), a related beetle that attacks 31 plant species in Florida, is Fusarium solani (Mart.) Appel and Wr. (Ngoan et al. 1976).

ENVIRONMENTAL CONDITIONS OF ATTACK

X. germanus most often attacks under the following conditions:

1. The trees are young: 7-year-old red oak in Germany (Heidenreich 1960) and 6- to 7-year-old black walnut in the United States (Kessler 1974).

2. Weather conditions prior to attack are unfavorable to tree growth and conducive to insect outbreak: late spring frosts (Heidenreich 1960), summer droughts (Gauss 1960, Heidenreich 1960, 1964), and mild winters (Gauss 1960).

Table 1.--World List of host Plants of Xylosandrus germanus (Blandf.)

Host	Location	Source
Abies alba Mill.	Germany	Wichmann 1957
Acer pseudoplatanus L.	Germany	Gauss 1960
A. rubrum L.	U.S.	Hoffmann 1941
Alnus incana var. glauca Regel	Japan	Wichmann 1955b
A. glutinosa Gaertn.	Germany	Wichmann 1955b
A. tinctoria glabra Sar.	Japan	Wichmann 1955b
Benzoin thunbergii Sieb. & Zucc.	Japan, Korea, Formosa	Felt 1932
Betula verrucosa Ehrh.	Germany	Wichmann 1955b
Carpinus sp.	Japan	Groschke 1952
C. betulus L.	Germany	Wichmann 1955b
C. laxiflora (Sieb. & Zucc.) Bl.	Japan	Felt 1932
Carya sp.	U.S.	Hoffmann 1941
Castanea crenata Sieb. & Zucc.	Japan	Wichmann 1955b
Cinamomum sp.	S.E. Asia[1]	Wichmann 1955a
Diospyros sp.	Japan	Ueno 1960
Distylium sp.	S.E. Asia[1]	Wichmann 1955a
Eurya sp.	S.E. Asia[1]	Wichmann 1955a
Fagus sp.	U.S.	Hoffmann 1941
F. americana (= grandifolia Ehrh.)	North America	Wichmann 1955b
F. crenata Bl.	Japan	Wichmann 1955b
F. sieboldiana Endl.	Japan	Wichmann 1955b
F. silvatica L.	Germany	Wichmann 1955b
Juglans nigra L.	U.S.	Kessler 1974
J. regia L.	Germany	Wichmann 1955b
Lindera sp.	S.E. Asia[1]	Wichmann 1955a
Liriodendron tulipifera L.	U.S.	Anderson et al. 1978
Machilus sp.	S.E. Asia[1]	Wichmann 1955a
Morus sp.	Japan	Groschke 1952
M. abla (sic) L.	Japan	Kaneko 1967
Nyssa aquatica L.	U.S.	Schneider et al. 1969
Picea excelsa L.	Germany	Wichmann 1955b
Pinus resinosa Ait.	U.S.	Buchanan 1941
P. strobus L.	Germany	Wichmann 1955b
Prunus serotina Ehrh.	U.S.	Schneider et al. 1969
Pterocarya rhoifolia Sieb. & Zucc.	Japan	Wichmann 1955b
Quercus paucidendata Franch.	Japan	Wichmann 1955b
Q. pedunculata Ehrh.	Germany	Wichmann 1955b
Q. rubra L.	Germany	Heidenreich 1960
Q. sessiliflora Sm.	Germany	Wichmann 1955b
Rhus sp.	S.E. Asia[1]	Wichmann 1955a
R. radicans L.	U.S.	Hoffmann 1941
Robinia pseudoacacia L.	Germany	Wichmann 1955b
Shiia sp.	S.E. Asia[1]	Wichmann 1955a
Styrax japonicum Sieb. & Zucc.	Japan, Korea, Formosa	Felt 1932
Taxodium distichum (L.) Richard	U.S.	Schneider et al. 1969
Thea sp.	Japan	Groschke 1952
Toxicodendron sp.	U.S.	Bright 1968
Tsuga sp.	U.S.	Bright 1968
Ulmus americana L.	U.S.	Buchanan 1940
U. effusa Willd.	Germany	Wichmann 1955b
Vitis sp.	U.S.	Felt 1932

[1] S.E. Asia = China, Japan, Korea, Formosa.

3. High beetle populations exist in the vicinity of the attacked trees on freshly cut stumps, logs, or branches (Heidenreich 1960, 1964, Hoffmann 1941, Kessler 1974).

4. Moisture content of the attacked wood and relative humidity of the air are high (Hoffmann 1941, Groschke 1953, Heidenreich 1960).

IMPORTANCE TO BLACK WALNUT

Fisher et al. (1953) state that ambrosia beetles, in general, are not primarily responsible for the death of trees, even in the tropics where they cause considerable damage. Instead, their economic importance lies in the degrade of sawn timber that results from their galleries and staining of the wood. For black walnut the primary importance lies in the extra time, labor, and money required to prune out dead tops and to remove all but one healthy sprout from a tree affected by the Fusarium/X. germanus complex. In addition, several years of growth time may be lost.

Studies are continuing on X. germanus and its relations to Fusarium and to black walnut. Meanwhile, control measures suggested by Kessler (1974) are still applicable: remove pruned branches or dead trees from the vicinity of the plantation to prevent a beetle population build-up.

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GROUP DISCUSSION

LaMadeleine: You mentioned that you could not find any more ambrosia beetles here in Illinois so you went to North Carolina. What is your feeling on the impact of this dieback, Barb?

Weber: In North Carolina, I did a survey and in one year 30 percent of the trees suffered from dieback, apparently from the Fusarium/ambrosia beetle problem. The trees themselves die back to the ground or a few inches above the ground. The walnut grower must go in and cut the dead tree back all the way to the ground and leave one of the sprouts. The sprouts are usually fairly healthy; they don't seem to be attacked later on. And so the impact would be the fact that you are losing growth and the fact that the grower must spend extra time pruning and making sure that all the diseased trees are removed from the area.

LaMadeleine: You know of a couple of plantations--are you finding it in more and more areas?

Weber: The number of plantations now is probably half a dozen, most of them in Indiana. I have recently found a population of the ambrosia beetle here again in southern Illinois. North Carolina is also a location. Ken found Fusarium in Iowa and Missouri but did not see the ambrosia beetle. One of the major parts of my study is to try to determine if X. germanus really is carrying the Fusarium fungus into these trees or what the exact association is.

Payne: Does *Fusarium* also cause the wood to stain blue?

Weber: *Fusarium* causes a brown stain.

Shigo: Regarding this German work, I would need a lot of convincing to believe that *Shizophyllum commune* was a direct associate with your beetle, because it is such an aggressive fungus. It will come in any place there is dead wood. I know you cited it as German work, but I would think carefully on that one to really show that it was a direct associate.

Weber: The Germans state that they found the fungus and the beetles at the same time and imply an association but give no direct proof.

THE ETIOLOGY, DISTRIBUTION, EPIDEMIOLOGY, HISTOLOGY AND IMPACT OF BUTTERNUT CANKER IN WISCONSIN

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BSTRACT.--A canker disease of butternut which as first reported in Wisconsin in 1967 occurs hroughout much of the tree's natural range and s a serious threat to the survival of the pecies. Trees of all age and size classes, egardless of site conditions, are afflicted y multiple cankers which occur on all above-round woody plant parts. The causal agent of e disease is a fungus, Sirococcus species. lthough the fungus has occasionally been found sociated with small cankers on black walnut rowing in mixed stands with butternut, tificial inoculations in the greenhouse dicate that the fungus is weakly pathogenic black walnut.

Widespread dying of butternut first was ported in Wisconsin in 1967 (2, 7). The mber and extent of the diseased areas as well the deterioration of the dead trees indicated at the disease had been active for several ars. Canker-dieback since has been found roughout the range of butternut (1, 11), d the fungus pathogen has been isolated from seased specimens collected in Indiana, Iowa, higan, Minnesota, Missouri, Pennsylvania and sconsin. A "Pest Alert" announcing "butternut line" was issued in 1976 (12).

Although butternut is a minor species in Wisconsin (9), quality butternut is second only to walnut in economic value (5). In fact, Wisconsin ranks second in the amount of butternut found in the United States and is a major producer of butternut lumber for furniture, cabinets, and fine woodworking (8).

In the past, butternut has suffered from few diseases (3) or insect pests. Now, however, it appears that canker is a potential threat to butternut throughout its natural range (10, 1). In North and South Carolina, butternut has been essentially eliminated by the disease (1). Likewise, in southwestern Wisconsin, many stands have been decimated and butternut is a "threatened species". In disease survey plots, as many as 80% of butternuts were cankered and 32% were dead (6). In contrast, in several counties in northeastern Wisconsin, no cankered trees were discovered. At first, no cankered butternuts were reported in the northern states of New Hampshire and Vermont (1), but recent communications indicate that the disease is present.

In Wisconsin, cankers were found on all woody parts of diseased butternuts, including twigs, branches, stem and buttress roots. Stem cankers, usually many per tree, both separate and coalescing, occurred on all sides of the trunk, especially the lower portion. Trees of all ages and sizes, growing in mixed and relatively pure stands, on dry, infertile ridgetops or moist, fertile bottomlands were cankered. Infected trees occurred in local pockets or over extensive areas. Among the severely cankered butternuts, occasional butternuts appeared healthy. Whether these trees are resistant or escape must be determined. However, incipient cankers can be overlooked unless bark is removed to reveal the darkened wood beneath. So far, in one study plot, small twig and branch cankers have been detected on a few black walnuts growing in mixed stands with severely infected butternuts.

Diagnostic symptoms of butternut canker include discrete, elliptical cankers involving the bark and wood of twigs, branches, stems and even roots (4). Young cankers commonly originate at leaf scars, other natural openings, such as lenticels and stomates, buds, bark wounds including insect wounds, natural bark cracks, and occasionally at points apparently free of any injury. Older cankers on trunks are large, open or partly covered by shredded bark, vertically oriented and perennial. Some stem cankers have progressed for many years (up to 13 years) as evidenced by successive layers of lateral callus or by differences in annual ring counts. In many cases, their origin is unknown, but adventitious buds are present in the centers of some cankers.

Peeling the bark from trunks may disclose small, local areas of brown, inner bark, and later, black wood of undetected incipient cankers. Older cankers often bear shredded bark, frequently are bordered by callus layers, and may coalesce to girdle and kill large branches or stems. Branch suckers and trunk sprouts frequently develop below the girdled portion, are infected readily, and die shortly thereafter. Seasonal sprouts become infected in the fall soon after leaf fall, but remain symptomless during the winter. In the early spring, before budbreak (April, 1978), tiny, round, chocolate-brown lesions develop around lenticels and small, irregular lesions develop at leaf scars. Initially, only the outer bark is infected, but soon the wood is invaded. Within a couple of weeks, the outer bark loosens, blisters, ruptures, and rolls back exposing masses of black hyphal pegs arising from a thin black fungus stroma. Under moist conditions, millions of conidia are extruded in countless colorless cirri (tendrils) from pycnidia borne in the stroma among the hyphal pegs.

In infected suckers, twigs, and branches, walls of bark cells are degraded (thinned), macerated, and rapidly disintegrated completely, leaving only a dark brown, gummy residue which gives rise to a brown exudate. The fungus penetrates the cell walls intracellularly and progresses through the ray parenchyma into the xylem. It then spreads into the longitudinal parenchyma and eventually into other bark and wood tissues. In spring, an inky-black, watery exudate issues from canker fissures; later, in summer, sooty-black patches remain. Eventually, infected butternuts die. Little or no regeneration of butternut occurs in diseased areas (6).

Under the outer bark, the causal fungus (coded BN-5, and tentatively identified as a new *Sirococcus* species) forms a thin, black stroma from which hyphal pegs arise lifting the outermost bark layer (4). Among the pegs are globose to flattened, single or confluent pycnidi in which short conidiophores line the inner pycnidial surface and bear hyaline, two-celled, fusiform conidia. Tan, sticky spore masses are extruded as "globs" or as cirri, and spores are disseminated by splashing or blowing rain or mist (4, 11). The causal fungus is readily isolated on common media from both bark and wood grows best at 24-28° C in light or dark, forms hyphal pegs and pycnidia in culture, and sporulates profusely in the light or dark especially on thin, drying agar cultures. Inoculations of fresh wounds with mycelium, spore masses, or spore suspensions incite cankers on branches and stems of butternut and black walnut (*J. nigra* L. seedlings and saplings. Young, succulent tissue is especially susceptible. Stem cankers develop at 16, 20, 24, and 28° C, and often kill buttern seedlings within 2 weeks especially at 16 and 20 C. Inoculations of young, succulent, nonwounded butternut seedlings with conidia suspensions followed by 48 hours of misting incite necrotic lesions on leaves which quickly droop, wither, and abscise before or after the fungus invades stem tissue.

So far, the disease has been detected infrequently on black walnuts growing in mixed stands with severely infected butternuts, but artificial inoculations induce progressive and killing cankers on young black walnut seedlings. On inoculated walnut saplings, stem cankers progress slowly, and many appear to be walled-off by callus layers bordering the canker. Hopefully, black walnut will prove to be resistant. Otherwise, the increasing number of walnut plantings in the central states would be in grave danger.

Meanwhile, disease studies continue, while detection and appraisal surveys by state and federal agencies seek to determine the distribution and impact of butternut canker on forest stands and plantings. The formulation of effective control measures must await further information. However, black walnut should not be plant in close association with infected butternuts. I mixed stands, cankered butternuts should be removed immediately.

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GROUP DISCUSSION

Nicholls: What causes the exudate from the cankers?

Jutte: I think it is the remains of cell walls. There are a lot of extractives in the wood of walnut and butternut that occur in the cell walls. Also we must not forget the lignins which are degraded. The lignin residues plus the resins constitute much of the black material.

Kuntz: In very young cankers some of the exudate occurs as droplets of liquid. Dr. Jutte feels that this liquid may be produced as the result of tissue maceration by enzymatic action.

Shigo: Exudation is a common early symptom of many cankers. Nectria cankers can have the same thing.

A lot of cankers originate at insect punctures. Cricket punctures on maple often have a black spot as an early symptom.

Kuntz: I think it's not an accumulation of dark spores as we originally thought. I think it's a host reaction to injury.

Shigo: The Sirococcus fungus seems to do so many things that it worries me. I wonder if you may not have a complex of several organisms responsible for this disease. I would be very interested in seeing what the differences are in the histopathology of the twig and stem cankers. You said that one seemed to be walled off while the other was not. Another thing that concerns me is that you have a fungus that kills tissue and also causes cell wall dissolution. It's possible but it raises the question of whether several organisms could be involved.

Kuntz: In the early stages of canker development only Sirococcus is isolated. Succulent tissue, particularly at times when trees are either going into or out of dormancy, is very susceptible to infection by this fungus. In the greenhouse, seedlings are killed in ten days after inoculation with the fungus. They are girdled, necrotic, wilted and dead.

Shigo: In some ways this disease is similar to chestnut blight.

Kuntz: We draw the same comparison and, of course, some people think that chestnut blight has some characteristics of a vascular wilt as well.

Neely: The term hyphal peg intriques me. Normally something like that, as with oak wilt, is called a pressure cushion. The sycamore anthracnose fungus when it fruits on twigs produces what I call a pressure cushion; it is very similar to your hyphal peg and the anthracnose fungus also produces pycnidial cavities in exactly the same manner as what you are showing me here.

Kuntz: The Sirococcus hyphal peg is not a pressure cushion.

Neely: Why is it not?

Kuntz: It's a peg. It's like your finger--like a cone. It's function is to lift the outer bark.

Nair: We have not found spores developing on the hyphal pegs.

BUTTERNUT CANKER

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ABSTRACT.--Butternut (Juglans cinerea L.) is declining throughout much of its range primarily due to a new canker disease caused by a fungus species in the genus Sirococcus. The canker does not appear to pose a serious threat to black walnut (Juglans nigra L.), a close relative of butternut. Butternut trees are killed by multiple cankering of branches and tree trunks. The dying portions of the tree often are colonized by a secondary-invading fungus, Melanconis juglandis. In culture, benomyl showed the best activity against the Sirococcus fungus at low concentrations (0.1 ppm), chlorothalonil was effective at higher concentrations (1 ppm), and maneb was ineffective at all concentrations tested. Fungicide control will not be economically feasible except possibly in nurseries and plantations. However, cultural and genetic controls may be possible.

Butternut, also called white walnut, is losely related to black walnut. Although utternut wood is light, it can be stained to ook like black walnut. The wood has many ses including furniture, cabinets, fine wood- ork, and paneling. In fact, in many areas here quality butternut wood is available, it s second in economic value only to black walnut.

Butternut is a minor species in the esophytic climax forests on rich moist sites roughout the northern two-thirds of the Eastern nited States. Nowhere is butternut common and s frequency is declining primarily due to a rious canker disease first reported in 1967. cept for this canker, butternut does not seem t be susceptible to any serious disease. esumably, if the canker disease could be ntrolled, butternut could become a more preva- nt timber and nut-producing species. Butter- nt, if grown canker-free, could be planted in antations and handled similar to black walnut. fact, butternut has some advantages over black lnut: (1) it is less demanding in its site quirements and can be grown on poorer soils a (2) it is more cold resistant and can be wn farther north.

Recent surveys show that butternut canker is present throughout much of the butternut range. Trees of all ages are infected and cause multiple cankers to form on branches and trunks which together eventually girdle and kill the trees. In many cases, it may take several years before infected trees die. The canker, caused by a fungus in the genus Sirococcus, has already eliminated butternut as an important forest species in many areas. Because it is being eliminated from the natural ecosystem throughout much of its range, it is possible that butternut soon may become a threatened species (from U.S.F.S. State & Private Forestry Survey data). Thus, forest management recommendations for butternut will have to be carefully considered for the benefit and survival of this species.

DISSECTION OF BUTTERNUT TREES

To obtain some basic information on the Sirococcus canker, 18 butternut trees were dissected and evaluated in La Crosse, Dane, and Dunn Counties in Wisconsin between 1976 and 1978. The bark was peeled off trees to reveal the dark-colored cankers, which were highly visible on the light-colored wood (Figure 1). Then, the following data were recorded: tree height and age; percent crown dead; number of healthy, cankered, or dead branches; number of trunk cankers; age of oldest canker; average length and width of cankers; and the number of cankers associated with leaf scars or buds. The information obtained was useful in characterizing the frequency and distribution of cankers. The results clearly revealed that butternut trees contain multiple cankers on their branches and trunks which eventually girdle and kill them regardless of whether they are growing on good or poor sites.

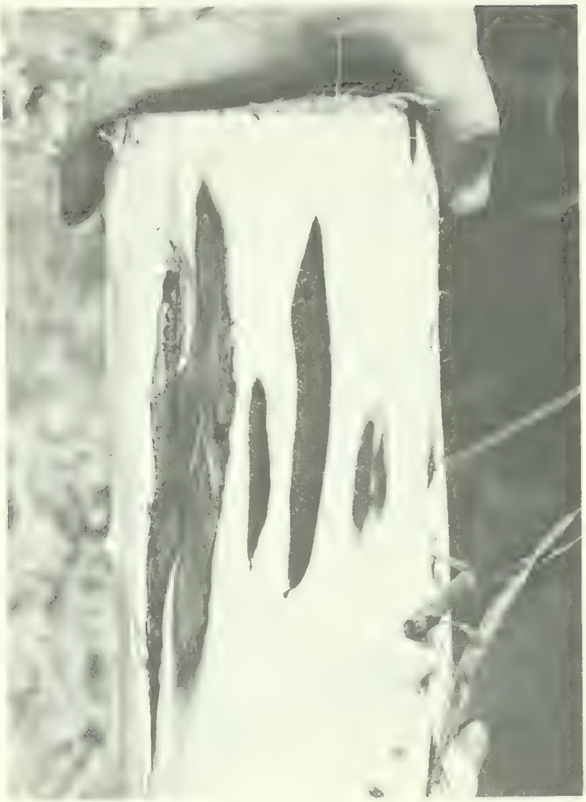

Figure 1.--Multiple dark-colored cankers are easily detected on infected butternut trees when bark is removed.

Trunk Cankers.--Infected butternut trees had numerous trunk cankers of different ages, many of which had coalesced. As many as 109 trunk cankers were observed on one tree but most infected trees averaged about 42 trunk cankers. Cankers were found on dissected trees ranging from 12- to 40-years old and from 10- to 53-feet-tall. Cankers were dark brown to black, elongate, and irregularly oriented on the trunk (Figure 1). Stem girdling or near girdling required the coalescence of several cankers. Cankers appeared to be perennial. Some cankers might have been inactive because they had successive vigorous callus growth around their margins, sometimes completely covering cankers. Canker ages ranged from 1 to 12 years, the latter with an origin of 1966 or about 1 year before the disease was first reported in Wisconsin. Most cankers were associated with adventitious buds, which probably serve as infection courts. Peeling the bark from the trunks was necessary to find the younger cankers but many older underlying cankers could easily be detected before peeling by sooty bark patches and loose, shredded bark resulting from an inky-black, watery exudate. Most infected trees had a partially dead crown but some infected trees had healthy-looking crowns.

Table 1.--Dissection results of seven butternut trees in Blue Mounds State Park, Dane County, Wisconsin, May 26, 1976

Tree number	D.b.h.	Height	Age	Crown dead	Healthy branches	Cankered branches	Dead branches	Trunk cankers	Age of oldest canker examined
	Inches	*Feet*	*Years*	*Percent*	*Number*	*Number*	*Number*	*Number*	*Years*
1	2	10	20	40	10	20	34	16	4
2	4	22	20	5	13	0	1	0	-
3	3	19	22	50	11	9	6	–[1]	4
4	3	23	--	10	1	18	4	3	4
5	5	25	30	20	--	--	18	21	4
6	8	41	40	40	12	7	14	50+	4
7	6	43	26	50	0	6	3	63	4

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[1] Many cankers coalesced.

Crown Symptoms and Branch Cankers.--Crown dieback was associated with extensive trunk cankering, branch cankering, or both and ranged from 0 to 75 percent (Tables 1 & 2). Most branch cankers originated at leaf scars or buds through which infection frequently occurred (Table 3). Young branch cankers were slightly sunken, elongate, and dark brown to black. Numerous branch cankers can kill branches and the epicormic sprouts that are produced when portions of the tree dies. The dying portions of the tree were often rapidly colonized by a secondary invading fungus, Melanconis juglandis.

One of the dissected trees had only one trunk canker but had many new branch cankers near the top of the tree indicating a major new infection of a previously healthy tree (Table 4).

Root Systems.--Roots of five trees were examined. Although cankers on some trees occurred on exposed buttress roots, infection did not appear to affect the rest of the root system. The fungus did not seem to be transmitted between trees through the root systems.

Table 3.--Average trunk and branch canker lengths and widths and their association with leaf scars or buds on three butternut trees examined in La Crosse and Dunn Counties, Wisconsin, spring 1978.

Tree[1]	Canker location	Average canker length	Average canker width	Cankers associated with leaf scars or buds
		La Crosse County		
Number		*mm*	*mm*	*Percent*
1	Trunk	158	31	70
	Branches	38	8	50
2	Trunk	166	27	80
	Branches	73	14	70
3	Trunk	82	23	--
	Branches	66	17	--
		Dunn County		
4	Trunk	--	--	--
	Branches	45	7	30
5	Trunk	108	11	--
	Branches	53	4	--
6	Trunk	173	26	50
	Branches	43	7	60

[1] Ten trunk and 10 branch cankers were examined on each tree.

Table 2.--Dissection results of five butternut trees on the Coulee Experimental Forest, La Crosse County, Wisconsin, May 18, 1977

ee nber	D.b.h.	Height	Age	Crown dead	Healthy branches	Cankered branches	Dead branches	Trunk cankers	Age of oldest canker examined	Average cankers/ branch
	Inches	*Feet*	*Years*	*Percent*	*Number*	*Number*	*Number*	*Number*	*Years*	*Number*
	4.7	25	21	10	6	8	9	33	5	5
	3.2	21	15	75	0	10	5	46	4	9
	4.2	26	20	60	1	19	10	57	6	6
4	3.8	23	20	20	6	20	21	39	6	2
5	4.7	26	16	0	12	0	4	0	-	0

Table 4.--Dissection results of three butternut trees in La Crosse and Dunn Counties, Wisconsin, spring, 1978

Tree	D.b.h.	Height	Age	Trunk cankers	Age of oldest canker examined
	Inches	*Feet*	*Years*	*Number*	*Years*
La Crosse County					
1[1]	2.5	23	13	36	5
2	2.2	19	12	33	5
3	4.4	29	23	109	7
Dunn County					
4	5.0	49	24	1[2]	5
5	4.8	47	26	52	11
6	8.2	53	32	73	12

[1] This tree appeared to be resistant because many cankers were walled off.

[2] Many small cankers present near top of tree on small branches.

Associated Insects.--Several unidentified insect larvae were found under the bark of some trees and discolored tree tissue similar to that caused by the fungus was found around them. Five isolations were made from the tissue to determine if this insect might be a vector or to see if the fungus might have gained entrance to the trees through wounds made by the insect. However, the fungus was not recovered from the discolored tissue and it is now believed that the tissue damage was caused by insect activity alone. Other insects associated with cankered trees were Acrobasis bud borers, weevils, spring tails, and thrips. Wounds caused by insects may serve as infection courts, but this was not adequately documented in this study.

The Sirococcus fungus produces spores in a sticky matrix and the cankers themselves secrete a material that oozes out onto the bark of trees. Insects may be attracted to this secretion and then transmit spores to healthy trees.

Resistance to Butternut Canker.--Two dissected butternut trees had no cankers even though they were surrounded by heavily infected trees (Tables 1 & 2). A third tree had 36 trunk cankers, but most of the cankers had healed over indicating some resistance (Table 4). These examples, along with other similar field observations, indicates that some trees may be genetically resistant to the disease. In this study, one black walnut was dissected and several others evaluated, but no infections were observed even where they were associated with heavily infected butternut. Other investigators have occasionally detected a few cankers on black walnut saplings, primarily those under stress. However, the canker does not seem to pose a serious threat to black walnut because black walnut appears to be highly resistant to the pathogen.

FUNGUS BIOLOGY

Spore release and dissemination.--In 1976 and 1977 vaseline-coated microscope slide spore traps were placed beneath and various distances from infected butternut trees in La Crosse and Dane Counties in Wisconsin. In addition, in 1977 spore traps were placed under butternut trees with dying branches in Marinette County, Wisconsin, where butternut canker has never been found. Traps were changed weekly from April to October and at irregular intervals from November through March. All Sirococcus spores were counted with a microscope at 400X on three vertical strips on each slide to determine the number of spores trapped and duration of spore release during the year. Weather and host phenological data were also obtained at each site.

Spores were produced from early April unti late October in both 1976 and 1977 (Figures 2 & 3). Germinating spores were found the weeks of May 10, July 26, and August 23, 1976, which may indicate infections periods. Because no spores were found on traps during weeks with no rainfall, rainfall must be necessary for spore release. Spores were found on the furthest traps from an infected tree, 150 feet, so spores can be rainsplash- and wind-disseminated at least that far.

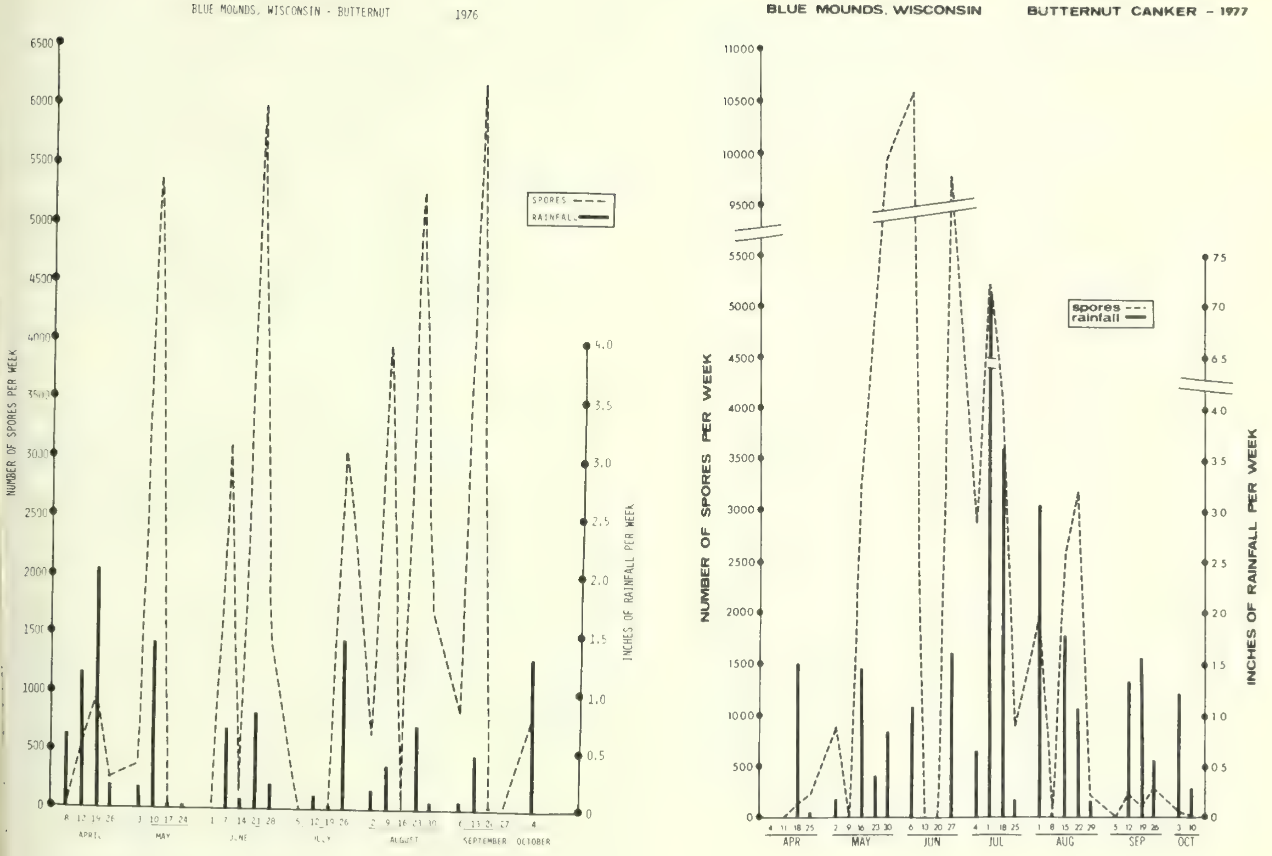

Figure 2.--Weekly butternut canker spore release and rainfall, Blue Mounds State Park, Dane County, Wisconsin, 1976 and 1977.

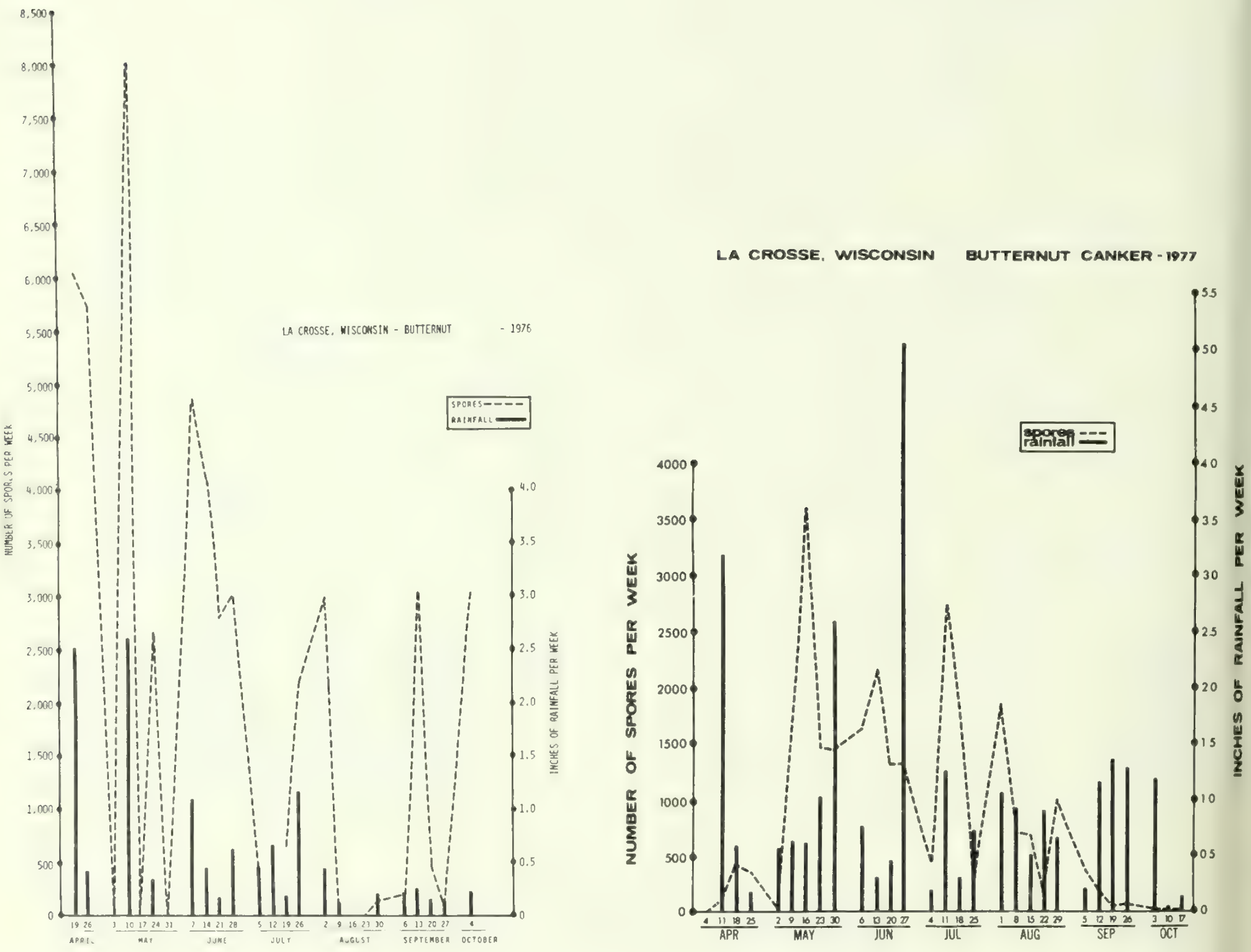

Figure 3.--Weekly butternut canker spore release and rainfall, Coulee Experimental Forest, La Crosse, Wisconsin, 1976 and 1977.

Despite the much-below normal 1976 rainfall, the total number of butternut canker spores trapped at two locations in southern Wisconsin were as follows:

Blue Mounds State Park

Spore trap location	Spore *Number*	Rainfall *Inches*
1. Under infected tree	35,159	12.34
2. Directly under cankers	3,880	
3. Directly under cankers	958	
4. In open, 18 feet from nearest infected tree	436	
Total	40,433	

Coulee Experimental Forest

Spore trap location	Spore *Number*	Rainfall *Inches*
1. Under infected tree	40,325	12.09
2. Directly under cankers	7,974	
3. Directly under cankers	1,696	
4. In open, 12 feet from nearest infected tree	377	
Total	50,372	

Rainfall was close to normal in 1977 and spore production and infection continued at a high level. The total number of butternut canker spores trapped in 1977 at the same 2 locations were as follows:

Blue Mounds State Park

Spore trap location	Spore *Number*	Rainfall *Inches*
1. Under infected tree	524	29.62
2. Under infected tree	60,925	
3. In open, 18 feet from nearest infected tree	54	
4. In open, 150 feet from nearest infected tree	13	
Total	61,516	

Coulee Experimental Forest

Spore trap location	Spore *Number*	Rainfall *Inches*
. Under infected tree	5,067	27.73
. Under infected tree	20,266	
. In open, 12 feet from nearest infected tree	403	
. In edge of red pine plantation, 35 feet from nearest infected tree	176	
Total	25,912	

The dying portions of many butternut trees ere rapidly colonized by a secondary-invading ngus, Melanconis juglandis (E. & E.) Graves. e spores of the imperfect stage of this ngus, M. oblongum, were also counted on the ore traps because of its close association and possible confusion with butternut canker. Major M. oblongum spore production occurred in May, June, and July, although some spores were released throughout the April to October period (Figures 4 & 5). Rainfall was also necessary for M. oblongum spore release.

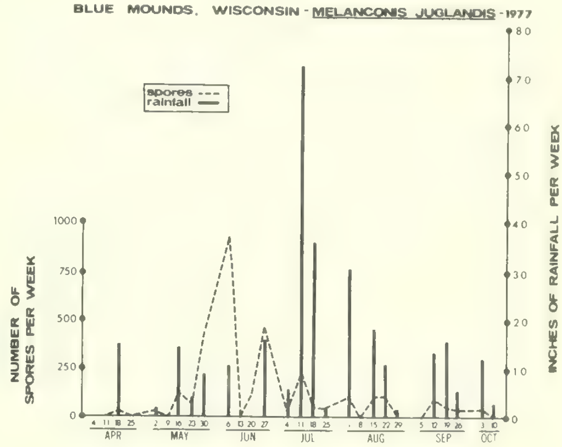

Figure 4.--Weekly Melanconis juglandis spore release and rainfall, Blue Mounds State Park, Dane County, Wisconsin, 1977.

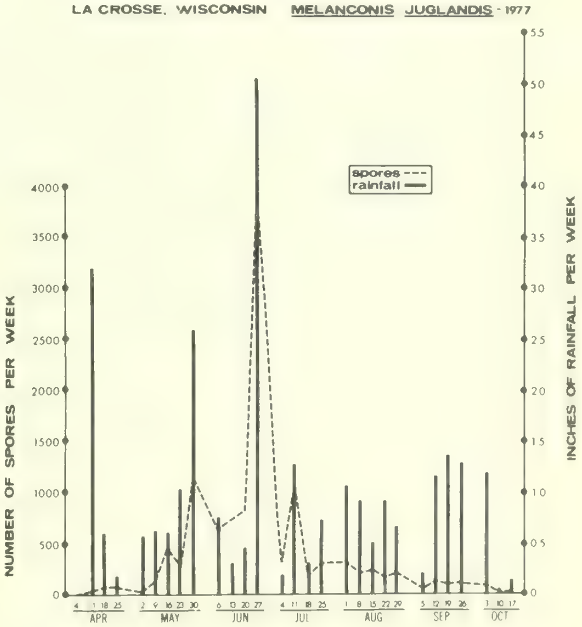

Figure 5.--Weekly Melanconis juglandis spore release and rainfall, Coulee Experimental Forest, La Crosse County, Wisconsin, 1977.

As expected, no Sirococcus spores were trapped in Marinette County where the canker has not yet been found. However, M. oblongum spores were trapped indicating its presence on dead branches of butternut trees in that area.

Phenology of Butternut.--Information on the phenological development of butternut is important for understanding the relation between time of host susceptibility and various stages of the fungus life cycle. Petiole growth began as early as April 11, leaflet growth ended as late as June 28, and autumn leaf fall occurred the last week in September and the first week in October (Table 5). Leaf scars and buds were important infection courts. Many cankers secreted an exudate during May and June and occasionally at other times during the growing season.

Butternut Inoculations with Sirococcus.--To determine pathogenicity, various techniques were used to inoculate butternut trees with Sirococcus spores produced in culture. Infection was confirmed by reisolating the fungus from infected tissue. The results showed that the fungus is a vigorous primary pathogen capable of infecting trees through wounded and unwounded plant tissue (Table 6).

Sirococcus Growth Study in Culture.--The fungus was incubated in vitro at 5, 10, 15, 20, 25, 30, and 35° C without light on potato dextrose agar to determine its optimum growth temperature. Optimum fungus growth occurred at about 30° C. Some growth did occur at 5° C, but none at 35°. In another test, cultures were grown under different light conditions to determine its effect on fungus sporulation and color. Spores were produced in culture in partial light at 20° C. (only temperature tested) and in total darkness at 20, 25, and 30° C. No spores were produced in total darkness at 5, 10, 15, and 35° C or in full light at 20° C (only temperature tested). The fungus was cream color when grown in total darkness, tan in partial light, and dark brown in full light. After 17 days of

Table 6.--Susceptibility of butternut seedlings to butternut canker fungus in greenhouse inoculation tests

(In numbers)

Treatment	Trees in test	Trees[1] infected	Tree healt
Spores applied by needle to wounds on stems and petioles	4	2	2
Spore suspension poured on leaves and stems, trees in plastic bags for 10 days[2]	3	3	0
Spore suspension poured on leaves and stems, scalpel wounds made, trees in plastic bags for 10 days	9	7	2
Trees wounded with scalpel, spore suspension applied to wound	4	0	4
Petiole bent to make small wound, spore suspension applied to wound	3	2	1
Total	23	14	9
Checks - Wounded	3	0	3
Unwounded	2	0	2
Total	5	0	5

[1] Confirmed by isolating fungus from infected tissue.

[2] Plastic bags were used to cover trees an provide optimum conditions for infection.

Table 5.--Phenological development of butternut in southern Wisconsin, 1976-1977

Location	Year	Petiole growth		Leaflet growth		Autumn defoliation completed
		Begun	Completed	Begun	Completed	
Dane County	1976	April 26	June 7	May 3	June 28	October 5
	1977	April 11	June 6	April 18	June 13	September 26
La Crosse	1976	April 19	May 24	May 3	June 7	October 5
County	1977	April 11	June 6	April 18	June 13	September 26

incubation, the fungus had an average diameter of 37 mm in total darkness, 27 mm in partial light, and 21 mm in full light. Only one Wisconsin isolate was used in this test, but the results show that temperature and light greatly affect fungus behavior. Therefore, researchers should document their notes carefully so that results can be accurately compared between workers.

Fungicide Tests.--Three fungicides were tested. Benomyl showed the best activity against the fungus at a low fungicide concentration (0.1 ppm), chlorothalonil was effective at a higher concentration (1 ppm), and maneb was ineffective at all concentrations tested (Table 7). Thus, at least two fungicides can be used for field testing in nurseries and plantations, if necessary. Unfortunately, it is unlikely that fungicides can economically be used to control this fungus because butternut trees are usually so ispersed and are so seldomly planted in plantaions.

Table 7.--Activity of three different fungicides on butternut canker in vitro

($\overline{X}$ fungus growth, mm)

Treatment[1]	Fungicide concentration (ppm)				
	1	0.5	0.25	0.1	0
aneb	21.8	25.0	22.7	24.3	--
lorothalonil	0	4.6	7.3	11.8	--
nomyl	0	0	0	0	--
eck	--	--	--	--	29.8

[1] Final readings were made after fungus ltures were incubated for 9 days at 20° C.

DISCUSSION

Forest managers who are concerned about Srococcus fungus need to know how best to mage their stands that contain butternut. Prhaps hazard zones of different harvest priority could be set up to salvage trees bfore they die and become useless. To do this w must know the detailed distribution and rate o spread of the canker disease. If it is dermined that butternut is a threatened species with the potential of it becoming an eangered species, totally different management pscriptions will have to be made with a pme objective being species survival.

Control of butternut canker will be extremely difficult, if not impossible. It is doubtful that chemical control will be economically practical except possibly in high value plantations and nurseries. Cultural controls may be useful in reducing the spread of the disease. For example, infected logs should not be shipped to mills in areas where butternut trees are healthy and the canker has not been found. Spores from such logs could serve as an inoculum source for adjacent healthy trees. Another useful practice is to prevent logging wounds during timber harvesting in areas where butternut are growing because wounds provide entry courts for the fungus.

Genetic resistance to the disease appears possible. In several areas where heavy mortality has occurred, a few apparently resistant (or possibly escape) trees have been found. These trees should be tested to see if they are truly resistant. If they are, seed can be collected from them and then the seedlings produced from this seed could be screened for resistance or susceptibility to the fungus. If resistance holds up, seedlings could be used to reestablish butternut populations in areas where the disease has eliminated or killed most of the butternut. It may also be possible to cross butternut and black walnut in the hopes of transferring the black walnut resistance to butternut but, of course, the reverse might occur. Although developing genetic resistance is often a complex and long term undertaking, it may offer the greatest possibility for saving the butternut.

Black walnut is highly resistant to the Sirococcus fungus but history has shown that, through evolution, genetic changes can occur in the pathogen, the host, or both that can increase the susceptibility of a previously resistant host. Thus, it is important to have a good understanding of the butternut canker disease complex and the impact it might have on the closely related black walnut. It would not be a good practice to plant walnut among or near infected butternut trees.

ACKNOWLEDGMENTS

Many people have contributed to the information contained in this paper. I would like to thank Al Prey, Bill Pratt, Gary Holzbauer, and Adrian Hagen, Wisconsin Department of Natural Resources, for maintaining spore traps and weather stations throughout the study. Michael Ostry, Kenneth J. Kessler, Jr., and Barbara Weber, North Central Forest Experiment Station; and James Kuntz, University of Wisconsin, all provided help and timely advice. More than 35 other people helped in the dissection and data collection on diseased butternut trees. Appreciation is extended to all those who participated in this team effort to gain an initial understanding of butternut canker.

GROUP DISCUSSION

Green: Since you are looking at cankers which seem to be of fairly recent origin, have you looked at any other contiguous species? What's the original inoculum source?

Nicholls: I think what has happened has been very subtle. Butternut has been disappearing slowly over many years. North Carolina, South Carolina, there's hardly a butternut left. The oldtimers say we had butternut all over the eastern part of this country.

Shigo: What you have said and shown is a dea ringer for what Eldon Ross did with ash decline at Syracuse. The canker looks almost exactly the same. He wa able to put Cytophoma on young ash seedlings and get infection. So seedling infection doesn't impress me too much because you can do that with a lot of fungi. Another point, you said, "The fungus kills because it girdles". You didn't show one slide where you had a girdle; does it reall girdle? You also said that the fungu is walling off, and these are your words "it looks as if its trying to wall it off". Every canker you showe was indeed walled off. You were able to date the cankers from 1 to 12 year which means they have been walled off for many years. Another point, if yo girdle a tree you don't get the kind of leaf crinkling that you showed.

Nicholls: I have seen coalescing cankers that d girdle trees. The ones you saw were on still living trees but if the olde trees are dissected coalescing canker are found. And wilting does occur jus as it does with the greenhouse inocul tions with Sirococcus.

Shigo: We talked about similarities of the butternut canker and the chestnut blight canker. A unique feature of chestnut blight as a canker disease is that it spreads circumferentially more than it does elliptically. Just about every butternut canker shown was an elliptical canker. They, for the most part, are not killer cankers. The only coalescing canker that comes close is found in the beech bark disease and even there only a small percentage of the trees are dying.

WOUND REACTIONS IN TWIGS OF BLACK WALNUT[1]

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ABSTRACT.--Since plants are not capable of replacing injured tissues, wounded areas are isolated from healthy portions of the plant by a number of anatomical and biochemical responses. Our anatomical studies of insect wounds of black walnut twigs have documented the injury responses and allowed us to make some generalizations about wound reactions in juvenile portions of the shoot system. The differences between the injury responses in twigs and trunks primarily reflect the obvious anatomical differences between juvenile and mature woody stems, i.e., wood comprises a much smaller proportion of the total stem volume in twigs. The compartmentalization of wounds in the wood of trunks and limbs has been well documented and is essentially the same in the wood of twigs. However, in twigs there is a considerable volume of additional tissues comprising the pith, the phloem, and the cortex, and in addition, parenchyma cells constitute a greater portion of newly formed (juvenile) wood. Depending on the location and severity of the wound, various combinations of wood compartmentalization, wound periderm formation, and cambial activity isolate the injured tissues and prevent pathogen invasion. The basic pattern of the response does not vary with the severity of the wound and is essentially similar for superficial treehopper oviposition wounds and for the severe wounds inflicted by walnut shoot borer, Acrobasis demotella. These responses generally reflect the processes by which trees protect twig tissues following the natural abscission of leaves, stems, and fruits.

The purpose of this presentation is to eview how the twigs of black walnut respond o injuries and to examine the effect of some ommon twig injuries on overall tree growth. e information in this presentation summarizes me of the results of an ongoing comprehensive udy of wound reactions in black walnut being arried on at the School of Forestry, Fisheries ad Wildlife, University of Missouri-Columbia, in cooperation with the USDA Forest Service. These studies include observations in mechanically, environmentally, and insect-inflicted wounds. Only the latter two categories concern the twigs since the first category was experimentally designed to study wood discoloration and compartmentalization in bole wood.

Although each insect wound was quite characteristic, the same types of anatomical and biochemical responses were observed in all instances. The response to the death of a terminal portion of a twig is quite similar whether caused by the feeding and tunneling of a shoot borer or a late frost. It is often said that with a very small bag of tricks nature achieves awe-inspiring variety. This report will review the little black bag of tricks with which a tree can respond to a wide variety of wounds. It will be seen that because of the effectiveness of the wound reactions, few twig wounds have a detrimental effect in themselves.

THE DIFFERENCES BETWEEN TWIGS AND TRUNKS

The differences between injury responses in twigs and trunks primarily reflect the obvious anatomical differences between juvenile and mature woody stems. Twigs have a considerable volume of non-woody tissues comprising the pith, phloem, and cortex. Gradually, through cambial activity, wood accumulates until it volumentrically comprises the vast majority of trunks. To the outside, the cambium is annually producing phloem, however, rather than continually accumulating, the older portions of the phloem are cut off by the formation of cork (periderm) and eventually shed. The functional phloem, old phloem, and corky tissues together comprise the bark. In addition to phloem, young twigs initially have a cortex between the vascular cylinder and the epidermis. The first periderm is formed in the outer cells of the cortex beneath the epidermis.

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[1] Not presented at Workshop.

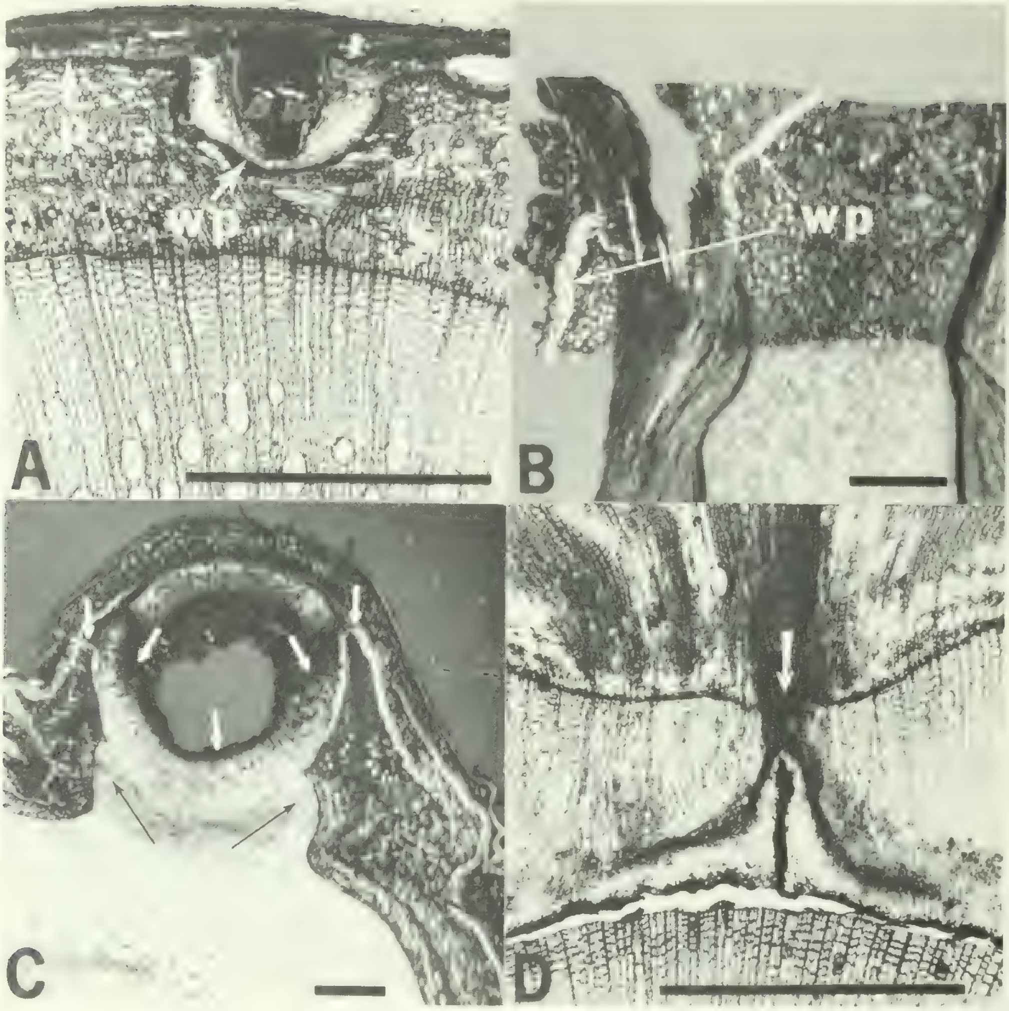

Figure 1.--Microscopic views of wound responses.

A. Wound periderm (WP) which is continuous with the regular periderm (P) has isolated superficial injury to the cortex and old phloem of a two-year-old twig. There was no cambial response to this wound. BAR equals 1 mm.

B. Longitudinally sectioned twig showing a portion of a diagonal plate of wound periderm (WP) viewed with polarized light. The characteristic birefringence is caused by the layered deposits of suberin and waxy substances in the periderm cell walls. Terminal portion of the twig (top, no shown) died following shoot borer injury. Wound periderm crosses, from left to right, the cortex and phloem, then skipping the xylem crosses the pith. Slight birefringence in intervening xylem indicates some deposition of suberin in ray parenchyma. Boundary between first-year pith and one-year-old pith (bottom) is evident because of the birefrigent secondary walls of the older cells. BAR equals 1 mm.

C. Cross section at the base of a dead twig showing isolation by a combination of wound periderm and wood compartmentalization (whit arrows). Dead tissue is at the top of this section. Lower left third of the frame is a developing lateral twig, compare with Fig. 2, D. Cambial activity would have eventually enclosed twig stub (black arrows) BAR equals 1 mm.

D. Cross section of a two-year-old twig showing callus formation and cambial activity following treehopper ovipositor injury. Split tissue at bottom indicates the position of cambium at the time of wounding, late summer Cambium reorganized toward central callus tissue and produced abnormal derivatives. Cambium, dark line of cells above center, hasn't reformed across small central portion of callus (arrow). BAR equals 1 mm.

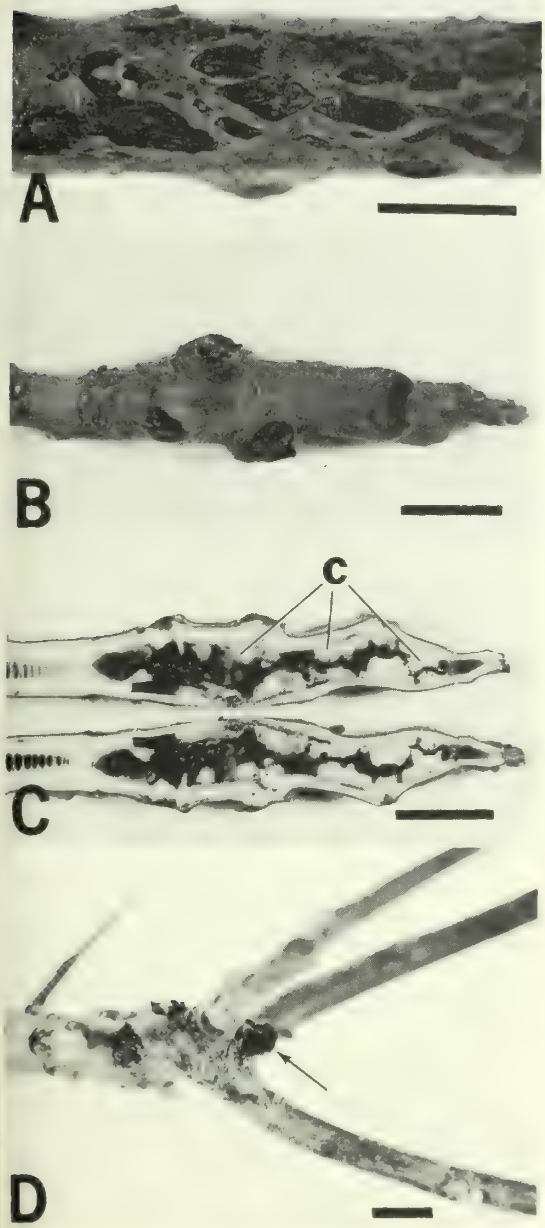

Figure 2.--Macroscopic views of wounded black walnut twigs.

A. One-year-old treehopper ovipositor scars on two-year-old twig. Internally the wounds have healed and would vary from something similar to Fig. 1, A to Fig. 1, D. BAR equals 1 cm.

B. Stunted, swollen one-year-old twig following attack by unidentified insect. BAR equals 1 cm.

C. Same twig as in B, split longitudinally to show development of callus (C) which causes the swelling. Black area consists of dead cells and insect detritus. Normal chambered pith is at left. BAR equals 1 cm.

D. Dead terminal twig stub (arrow) one year after shoot borer attack. Note the whorl of developing lateral twigs. BAR equals 1 cm.

WOUND RESPONSES

Since plants are not capable of replacing jured tissues, wounded areas are isolated om healthy portions of the plant by a number anatomical and biochemical responses. The rtex and pith are largely composed of parenchy- cells. The phloem and young wood also con- in a considerable amount of both axially and dially oriented parenchyma cells. It is these lls which are capable of a trauma-induced differentiation giving rise to callus tissue, cork or vessel tyloses. The parenchyma cells plus cambial activity are therefore responsible for isolating injuries and restoring normal stem structure and function. Injured tissues outside the cambium are isolated and eventually lost with exfoliating cork, along with the old cortex and phloem. However, inside the cambium injured tissues are isolated but never lost.

Deposition of protective substances and cork formation.--The deposition of suberin and other substances in cells surrounding a wound is a biochemical reaction that appears to protect underlying tissues. This reaction is more noticeable in the cortex, phloem, and pith than in the wood, probably because of the diffuse arrangement of live cells in young wood. This is a plant's most immediate response to injury.

In the cortex, phloem, and pith a periderm is formed underlying the zone of deposition. It is probable that the deposition of suberin and/or other substances (phenolic) must preceed periderm formation and provides the proper cellular climate for the dedifferentiation of parenchyma cells leading to periderm formation (Mullick, 1977). The wound periderm is usually continuous externally with the normal periderm, and, if the wound is deep enough, internally with the cambium (Fig. 1).

Cambial activity and callus formation.--The cambium reacts to a nearby wound by producing abnormal derivatives. The rate of cell divisions is usually increased, especially if the cell division rate has naturally slowed down or ceased toward the end of a growing season. If the cambium is directly injured there is a proliferation by cells near the wound producing a callus composed of parenchyma cells (Fig. 1, D). Not only does the callus close the wound, but a new vascular cambium and cork cambium are established in this tissue (Fig. 1, D). It is also possible for pith cells remaining after insect feeding to form a callus which refills the hollow pith (Fig. 2, C). In some cases the proliferation of callus can cause the twigs to swell and gives the appearance of a gall-like formation (Fig. 2, B-C).

Wood and compartmentalization.--The compartmental nature of wood structure and wound reactions has been well documented (Shigo, 1975, 1976; Shigo and Marx, 1977) and is essentially the same in the juvenile wood of twigs. Juvenile wood has the same compartmental structure, although, in first-year wood the inner wall 2 (tangential wall of latewood in mature wood) is formed by pith parenchyma rather than the terminal parenchyma and latewood fiber of the previous year's growth. Compartmentalization in juvenile wood is very good because of a higher proportion of parenchyma cells than in mature wood, and the high proportion of these cells that are alive and capable of reacting to injury. As each year's wood becomes a year older, the number of live parenchyma cells decreases until the wood is nearly completely dead and incapable of a positive significant response to injury.

DETRIMENTAL EFFECTS OF INSECT WOUNDS

In general the wound responses of black walnut twigs are very good and the detrimental effect to the tree are minimal. A treehopper, Enchenopa binotata produced ovipositor wounds that were essentially superficial, completely healing in a single season, although an external scar persisted (Armstrong, Kearby, and McGinnes, unpublished report) (Fig. 2, A). These wounds leave a small callus inclusion in the wood, but don't seem to be a point of entry for pathogenic organisms.

An as yet unidentified insect produced somewhat more serious wounds, tunneling and feeding in the pith of elongating black walnut twigs. The resulting proliferation of callus tissue caused a gall-like bulge at the base of a stunted twig (Fig. 2, B-C). On a mature tree the twig deformities would be negligable, while a young tree's form could be adversely affected.

The most serious wound studied was caused by the feeding and tunneling of a walnut shoot borer, Acrobasis demotella (Kearby, 1978). Expanding twigs attacked by the larvae of A. demotella usually died. An effective wound response isolated the dead terminal and prevent entry of pathogenic organisms. Continued cambi activity will eventually enclose the dead twig stub in the same manner that branch stubs are healed. However, the loss of the terminal bud results in the elongation and development of usually several lateral buds (Fig. 2, D). In young trees this produces whorled, busy branchi pattern which can be very detrimental to wood production by reducing the length or at least prolonging the time necessary to grow an adequa length of clear bole.

Frost damage, if severe, is quite similar to shoot borer damage, however, since frost damage is not specific the effect varies. The hollow twigs left by the shoot borer are easily identified and don't occur in a widespread, general pattern like frost damage.

SUMMARY

Current research finding of response to injury in young twigs of black walnut indicate that:

1. Mechanism of response appears the same regardless of environmental influence; however, each causative factor has its own characteristi pattern. Treehopper damage is minimal while shoot borer damage and frost damage are more severe. Frost damage produces a greater variety (range) of effects which seem plausible in view of wide range of "severe" frost exposures possible.

2. The anatomical response pattern can be well documented--the biochemical responses are not completely understood to date and more research is needed in this area.

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PATTERNS OF DISCOLORED AND DECAYED WOOD IN BLACK WALNUT

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ABSTRACT.--*After wounding, trees compartmentalize injured and infected tissues. This process appears to be under genetic control. How effectively a tree compartmentalizes injured and infected tissues is a major factor that determines the limits or configuration of the defect column. The microorganisms involved in the successional patterns are major factors that determine the rate of the discoloration and decay processes. Discolored and decayed wood in black walnut can be detected by the Shigometer. New information about compartmentalization, succession, and the Shigometer gives new opportunities to regulate and to detect discolored and decayed wood in black walnut.*

Black walnut takes us from the forest to the single tree. The extremely high prices paid for selected single trees during the last few years have caused increased concern for internal defects caused by discolored and decayed wood. Buyers cannot use broad estimates of defect for great numbers of trees in a forest when they need to determine the exact internal condition of selected single trees. This new demand for increased accuracy must be met with new information from research. The same situation obtains for the growers. They need better information from research on how to grow higher quality trees with fewer defects.

For the last 19 years at the Northeastern Forest Experiment Station, research on discoloration and decay in living trees has anticipated these demands, and more information is now available to help the growers and the buyers.

WHAT'S NEW?

The person who wants to grow high quality, high priced, defect-free black walnut trees has two very important questions for the research pathologists who are studying defects: What have you done that will help me now? What are you doing that will continue to help me as new problems arise?

In answer to the first question, we now have an expanded concept of tree decay to serve as a basis for decision making; and, to move this concept out to the person in the field, we have a new model system called CODIT that will help explain the development and configuration of defects in trees. We also have new electrical equipment that will detect internal defects in trees.

This information also helps to clarify misconceptions about the tree decay process. In so doing, it helps to refute some myths such as frost causes frost cracks, wind causes ring shakes, and that decay progresses indiscriminately through heartwood.

In answer to the second question, we now have new information that suggests that the wound response is under genetic control. This means that we may be able to start selecting for decay-resistant trees.

ROLE OF THE RESEARCHER

The researcher has the responsibility to package this new information together with sound older information in a form that will reach the people who need it. The people who ask for the information have the responsibility to use it.

Too often researchers are criticized for not providing user groups with the information they need. This may be so in some areas, but it is not so with the subject of internal defect of trees--the information is available. It has been published and packaged in many different forms to reach many user groups, so the intent here is to give only brief summaries of available information. Please contact the author for additional details.

DEFECTS AND VALUES

Discolored and decayed wood are major defects that affect the value of the black walnut tree. A tree that looks fine from the outside may have many internal defects. The converse may also be true. How is a buyer to know what the actual internal condition is? Research has provided a new device to help; it is called the Shigometer. When used correctly, this electrical pulse resistance meter provides information that can be interpreted to determine the internal condition of a tree. The meter can also be used to determine relative growth rates in trees, and this information can be used to help select trees for thinning.

The grower wants to know how to grow trees with fewer defects. Before this can be done, the grower must understand how defects start and how they continue to develop.

The classical concept of tree decay lacks information on many essential phases of the decay process. The new concept includes compartmentalization--the response of the tree to wounding; and succession--the presence of many microorganisms in the processes that result in discolored and decayed wood.

A simple model system called CODIT--an acronym for Compartmentalization Of Decay In Trees--has been developed. The system explains ow a tree is compartmented and how it reacts fter wounding by compartmentalizing the injured nd infected wood. The system is based on four numbers: 1, 2, 3, and 4, which denote "walls" n the model. Each growth ring is divided into ompartments. After wounding, the "walls" begin o confine the injured and infected wood. Walls are the horizontal top and bottom of the com-artments. Walls 2 are the tangential sides. alls 3 are the radial sides. Wall 4 is the arrier zone formed by the cambium after wounding. he CODIT model can serve as a basis for under-anding the development of defects in a wide ariety of trees--deciduous hardwoods, and onifers of the temperate and tropical forests.

When a person uses the CODIT model along with external indicators and the Shigometer, he can determine the internal condition of the tree with great accuracy. And greater accuracy is required now because of the increasing emphasis o the single tree. This is how better concepts, better methods, better tools, and better recommendations can be used to help growers and buyers.

DISCOLORED WOOD, DECAYED WOOD

We know that wounds start the processes that lead to discolored and decayed wood (Fig. 1). In discolored wood, the cell contents and walls have been altered in such a way that the color is different from nonaltered, healthy wood. There is no loss in strength. In decayed wood, cell walls have been digested. There is loss in strength.

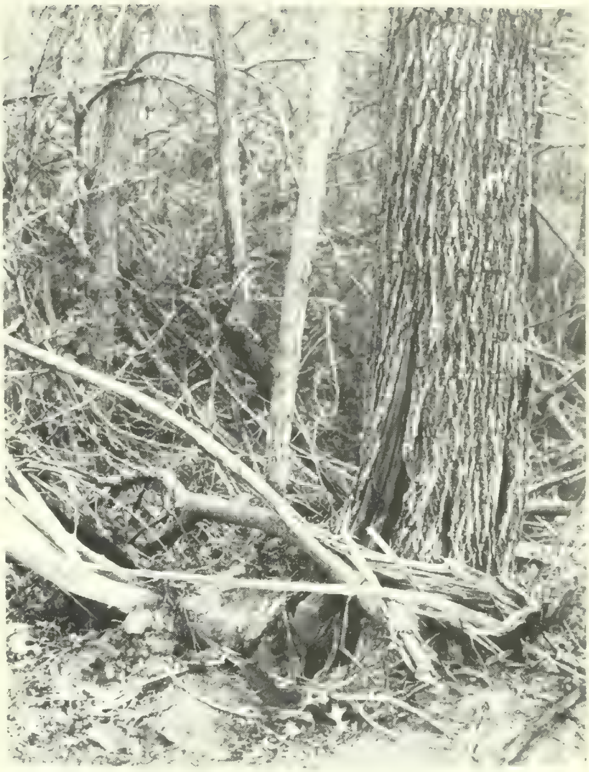


Figure 1.--Logging injury at base of black walnut tree. Mechanical wounds start the processes that lead to discolored and decayed wood. Wounds must be prevented if high quality trees are desired.

A wide variety of microorganisms are involved in the processes that result in discolored and decayed wood: decay-causing fungi, non decay-causing fungi, and bacteria. They infect wounds in succession where bacteria and non decay-causing fungi may be the first microorganisms to interact with the tree; while in other cases, the decay-causing fungi may be the first. Regardless of the exact sequence, it is not the heartwood-rotting fungi alone, but many microorganisms that are involved in the infection processes.

A wound exposes injured wood. The tree reacts to the injury by forming a chemical protective barrier beneath and around the injured wood. Slight alterations in the color of the wood could result from these processes. When some microorganisms are able to surmount the protective barriers set up by the tree, the tree responds further to this infection and the altered color of the wood may be further intensified. These processes occur in sapwood and heartwood. It is often difficult to recognize slight changes in the color of the dark heartwood of black walnut, but discolored heartwood is common.

The columns of discolored wood in the heartwood often result in a banding pattern. The bands or columns of discolored wood are associated with wounds. The most common wound is the branch stub. All trees have branches, and all trees will have some dead branches. The branching habit and the formation of stubs are major factors that affect the pattern of discolored wood in the heartwood. This means that black walnut trees with large, dying branches will have many columns of dark discolored wood in the heartwood.

TREES REACT TO WOUNDS

The wounded tree reacts not only in a chemical way, but also in an anatomical way. A tree is a highly compartmented plant. After wounding, the tree responds by confining, walling-off, or compartmentalizing the injured and infected tissues in the sapwood and heartwood.

After wounding, the living cambium begins to form a new tissue--the barrier zone. It is an anatomical and a chemical zone that separates the tissues present at the time of wounding from those that will continue to form. When wounds are inflicted during the dormant period, the cambium begins to form the barrier zone when growth is resumed. The extent of the barrier zone is determined by many factors: the size, position, and severity of the wound, and the genetic capacity of the tree to respond to the injury. The barrier zone is a highly protective tissue for the tree, but it serves as a plane of weakness when mechanical stresses occur.

BARRIER ZONE AND DEFECTS

The barrier zone is the primary site for ring shakes, which in turn are the beginning of many radial cracks commonly called "frost cracks". Most ring shakes and frost cracks are associated with wounds. Most frost cracks start from the inside and develop outward. The frost or cold serves to stress the wood, and it cracks along the internal plane of weakness that was set up by a wound. It must be remembered that branch stubs are wounds, and every tree will have some wounds of this type. Not all wounds lead to ring shakes and frost cracks, but all ring shakes and frost cracks observed by the author have been associated with wounds.

PRUNING WOUNDS

Wounds caused by faulty pruning can serve as starting points for many internal defects in black walnut--bands of dark discolored wood, ring shakes, and even radial seams. Pruning is definitely not a "cure all" for black walnut (Fig. 2) If pruning is to be done, it must be started earl in the life of the tree and continued as needed until the tree reaches early maturity. Great care must be taken if trees over 8 inches in diameter are to be pruned for the first time. When this is done, a person must understand the "trade offs". When dead and dying branches are pruned, the callus branch collar must not be cut flush with the stem. This will cause a severe wound that could lead to large columns of discolored wood, and possible ring shakes (Fig. 3). When callus branch collars are present, the branc should be cut in such a way that the collar is no injured. The trade off is a shorter length but higher quality of clear stem. Another reason why we must take another look at pruning is because of the chain saw. The powerful, lightweight chain saw makes it too easy to make long, flush cuts through callus branch collars.

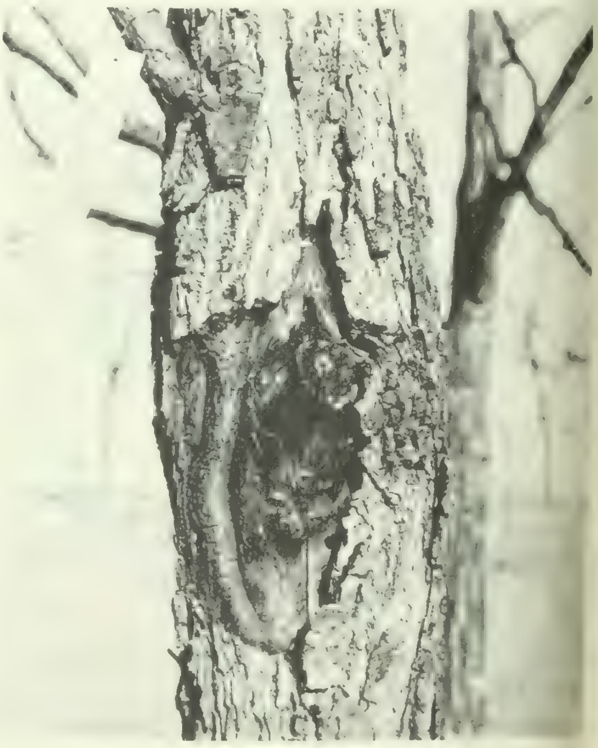
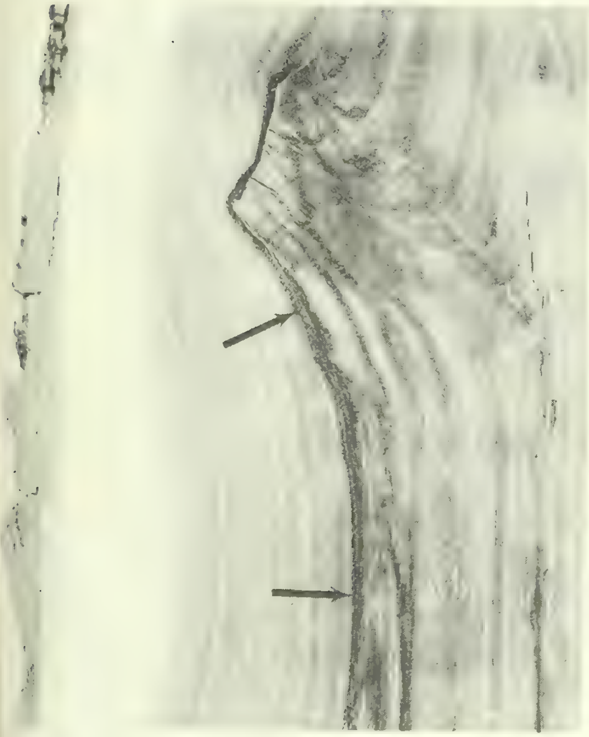


Figure 2.--Pruning is not a "cure all". Dieback around some pruning cuts greatly enlarge the wound.



igure 3.--The dark band of discolored heartwood formed after the branch was pruned. The cambium formed a barrier zone (arrows) that separated wood present at the time of wounding from wood that formed subsequently. The barrier zone is sometimes the site of ring shakes.

As a result of poor pruning techniques and he increased number of injuries to the boles of rees caused by the use of more heavy equipment round trees, the problem of discolored wood will ecome more urgent. It is relatively easy to ecognize decayed wood, but it is often very ifficult to assess the amount of discolored od in a tree or log until it is made into eneer. Then it is too late!

GENETICS OF THE WOUND RESPONSE

Wound one black walnut tree, and it comrtmentalizes the discolored and decayed wood a very small volume (Fig. 4). Wound another ack walnut tree in the same way at the same me, and the volume of discolored and decayed od may be many times greater than that of the her tree. Why? It appears that the compartntalizing capacity of individual trees is under genetic control. This does not mean that decay will not develop in a tree, but it may be confined to a very small volume in one tree and extend to a very large volume in another tree of the same species. From experiments on other tree species, it appears that the compartmentalizing capacity is not associated with growth rate. A simple wounding technique has been developed to determine the relative compartmentalizing capacity of a tree. The tree is wounded with a drill bit several times. After a set time, the condition of the wood above the wound is determined with the Shigometer. Trees that have very small columns can be easily identified, and then used as parents.

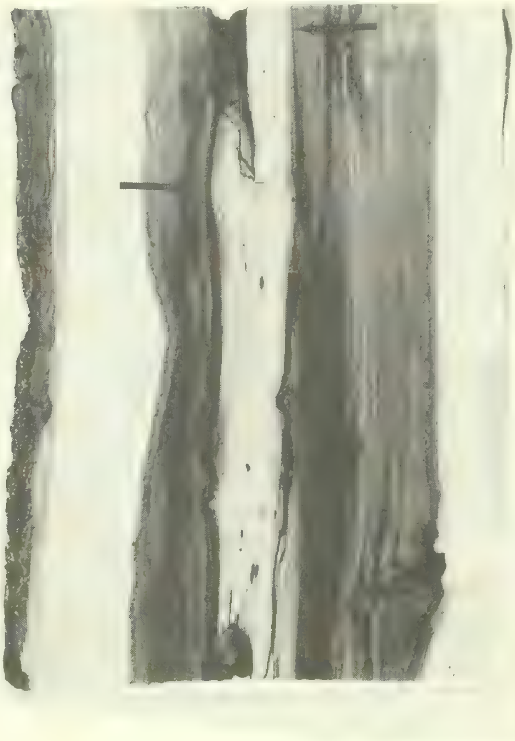


Figure 4.--Compartmentalization of decay in heartwood (arrows). The decay will not spread out to the surrounding heartwood.

WHAT NOW?

We must move available information into use. Defects don't just happen--we must reduce mechanical wounds and we must reassess pruning techniques. Also, we must use new methods to detect defects, and begin to select trees that have a strong compartmentalizing capacity.

ACKNOWLEDGMENT

I thank Paul Szopa, University of Missouri, School of Forestry, Columbia, Missouri for Figures 4 and 5.

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GROUP DISCUSSION

Payne: You say that trunk cracks once established stay established? Why can't they callus over?

Shigo: They will in some trees after 2 to 4 years. But it is almost inevitable that at some later time a cold spell or some other stress will cause reopening.

Kuntz: You talk about disease reactions in terms of barriers to decay columns and the possibility of selecting trees that have this capacity to compartmentalize. Do you see any evidence that this type of compartmentalization is effective against canker and vascular wilt organisms?

Shigo: I don't have the answer to this. But we do know this: you drill holes in trees and you will find that certain trees will have much more dieback around the holes. In some ways that might be likened to a canker. This might be related to why cankers spread more on some trees than others.

Kuntz: Is compartmentalization more common in white oaks than red oaks?

Shigo: I will say not more common. I would say it was more effective in the whit oaks than in the red oaks.

Kuntz: When we were looking at grafts on oak root systems we often noticed example where decay came in the lateral roots and when it encountered a graft; that as far as it went. Why didn't it continue on?

Shigo: Because you have a new tree. In a sense you have a new group of compartments at a graft union.

Nicholls: Could you clarify callus tissue and barrier tissue?

Shigo: Callus tissue is the undifferentiated tissue found after a tree is wounded. It can be primarily around a wound where it's going to be a next year's growth ring. Because the cells are on the outside and do not have equal pressures on their sides they continu to grow without definite form. The barrier zone is formed far above and below the wound site and will not be associated with an increase in the amount of wood produced. The barrier zone is both a chemical and anatomica tissue. You cannot see the barrier zone. We know it more as a model. There are at least six laboratories who are trying to answer your questio "what is the barrier zone?". We know that it is a phenol rich zone--it's an area where changes of lignins occur, it's an area with all kinds of metabolic shunts.

Kuntz: Are tree injections practical?

Shigo: We must use the present injection methods very carefully. For example with Dutch elm disease after injectin each year for four or five years you run out of space for injection holes. You say put them at the base of the tree--you run out of the base of the tree after five years, too.

Nair: Why does this bother you when you say every ring is a new tree?

Shigo: The elm tree has a 15-25 ring of sapwood. When you reduce that sapwood down to one ring, and that ring is not continuous because of the cankering around many of the holes, you may have a growth ring that is only 10% alive. Then when you need to inject the theraputic material into the tree you've got one-tenth of a growth ring into which to move the material.

Nair: As long as you don't girdle it, it will move.

Shigo: Yes, it will move, but you have to use all kinds of pressure. Remember you can't move materials through dead wood, and discolored wood in this place is dead wood.

PECAN PEST RESEARCH

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ABSTRACT.--*The rapid growth of the pecan industry has brought about new problems in insect control. With the trend away from native stands where every tree is genetically different toward groves of uniform cultivars, the damage caused by insects is more severe. The total yield as well as nut size and quality can be reduced by 20 or more species of insects and mites. These pests also reduce the vitality of pecan trees by damaging the leaves, buds, fruit, twigs, branches, bark, and even roots. This feeding damage can injure the tree so that developing pecans cannot mature, or it can damage the tree to such an extent that pecan production is drastically reduced the following year. Control is often difficult because of the complexity and size of the arthropod fauna as well as the large tree size. The pests multiply rapidly because large acreages of pecan groves provide an abundance of the food they prefer. Species that were not common in the past have moved from hickories and other host plants.*

Man's monoculture of plants has made production economically and physically sound but at the expense of tremendous modifications in the natural environment. Concentrated food production has made knowledge about the technology of pest control exceedingly important. With the current trend away from native stands where every tree is genetically different toward groves of uniform cultivars, the damage caused by insects is more severe. The pests multiply rapidly because large acreages of trees provide an abundance of the food they prefer. Species that were not common in the past have moved to pecan trees from hickories and from other host plants. Where row after row of single nut crop is produced, it is no wonder that new pests find happy hunting grounds. Under these conditions, the balance of natural control is upset, and pest populations build up rapidly if left unchecked.

There are at least 180 species of insects and mites that feed upon the wood, foliage, shoots, bark, or nuts of pecan and hickory. Most of the important insects in the Pecan Belt[1] are also serious pests on northern pecans and other hickory species; occasionally some species attack walnut and other fruit trees. More than 20 species of insects affect pecan production by feeding on the fruit or by injuring the tree so severely that developing pecans may not mature; or they can damage the tree to such an extent that pecan production is drastically reduced the following year. These pest species usually require some method of control to protect the crop. We present here a brief discussion of biology, damage, distribution, and control for approximately 20 major pecan pests.

OBSCURE SCALE

The obscure scale, Melanaspis obscura (Comstock), is found in most areas of the Pecan Belt, and it is a sufficiently serious pest of pecans in Texas, Louisiana, Arkansas, and Mississippi, so that chemical control is often necessary. Its body, about one-eighth inch long, is covered with a circular dark-gray scalelike substance. Its body coloration is similar to that of the tree bark, which makes detection difficult. It attacks both branches and tree trunk. The bark of heavily infested branches appears roughened or scaly.

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[1] The pecan is grown principally across the southern United States in a belt that includes Alabama, Arizona, Arkansas, Florida, Georgia, Louisiana, Mississippi, New Mexico, Oklahoma, South Carolina, and Texas.

Since scale sucks the sap from plant tissues, it can gradually kill branches less than 3 inches in diameter. Larger branches are seldom killed, though they may be so weakened that they will not produce a normal crop. Slow, progressive destruction of infested branches reduces the number of fruiting shoots and weakens the tree which makes it subject to attack by wood boring insects.

Scale produces only one generation each year. The young, called crawlers, are present from about the middle of May until early August. Soon after they hatch, the crawlers settle on the bark, insert their beaks, and begin to form their waxy scale coverings. They gradually increase in size and, except for the adult males, do not move around. Female scales overwinter under their scaly covering on bark.

Control: Chemical control of scales is often necessary. A single oil spray in the early spring while the tree is still dormant will keep this pest under control.

PHYLLOXERA

Two species, *Phylloxera notabilis* Pergande and *P. devastatrix* Pergande, are found in almost all sections of the Pecan Belt, from Georgia in the east through Texas in the west. Both species overwinter in the egg stage. When they hatch in the spring, these small soft-bodied sucking insects feed on new plant growth, and cause tumorlike swellings or galls, one-tenth to 1 inch in diameter, to appear on leaves, leafstalks, succulent shoots, and nuts. The pecan hylloxera, *P. devastatrix*, is the most damaging; his insect causes malformed, weakened shoots hat finally die. Severe infestations can estroy entire trees. Serious damage has been eported in Arkansas, Louisiana, Mississippi, klahoma, and Texas.

Control: Spray trees thoroughly during he delayed dormant period or spray before he buds of earliest varieties show 1 inch of ew growth.

PECAN BUD MOTH

The larvae of the pecan bud moth, *Gretchena lliana* (Slingerland), often cause serious mage to pecan nursery stock by feeding on rminal buds and foliage. The damage causes cessive branching and stunted growth in young can trees and sometimes loss of the grafted d. The larvae occasionally defoliate large can trees, feed on young nuts in spring, and infest the shucks in fall. The insect overwinters as an adult. The moths begin laying eggs on the twigs near buds when the buds open in spring. When foliage appears, they lay more eggs on the upper surfaces of the leaves. The mature larvae, about one-half inch long, are creamy to dirty white at first, becoming yellowish green with dark-brown heads and necks. After they feed for 25 days, they pupate in rolled-up leaves or infested buds, but occasionally under bark scales. There are probably five or six generations each year.

Control: Vigorous young nursery trees kept healthy by proper water, cultivation, and fertilization usually recover from bud moth attack better than weaker ones. Control is usually necessary in nurseries but seldom necessary in bearing groves.

PECAN NUT CASEBEARER

The pecan nut casebearer, the larva of the moth *Acrobasis nuxvorella* Neunzig, causes damage throughout the Pecan Belt. Only Arizona and California have escaped this pecan pest. Losses vary with the size of the crop. A light-to-moderate infestation in a heavy set of nuts may merely provide desirable thinning, but in a light crop most nuts may be destroyed.

Partly grown casebearers pass the winter in small, tightly woven cocoons called hibernacula that are usually found where a bud joins the stem and under bark on the limbs and trunk. The casebearers become active in spring about the time the buds begin to open. They feed for a short time on buds and then bore into the young tender shoots, where they pupate. The moths usually emerge in May and are most numerous about the time of nut set. They lay greenish-white oval eggs on the blossom end of the nut, usually near the base of the calyx lobes. Commonly, only one or two eggs are laid in a cluster of nuts.

The first-generation larvae cause most of the damage in May and June. These newly hatched casebearers descend from the nut clusters to feed on the buds just below. A few days later, they return to the clusters and attack the newly set nuts, normally entering them at the stem end. Infested nuts are held together by silken threads and are easily recognized by the conspicuous frass cast out by the larvae. In the course of development, a single casebearer of this generation may destroy all the nuts in a cluster. Larvae mature and pupate in one of the last nuts they attack.

Second-generation moths appear in late June and early July. Larvae of this generation also attack the nuts, but the loss is less because the nuts are larger, and the individual casebearer requires fewer nuts for its development.

Control: Growers should spray with the recommended pesticides if over 3 percent of the previous year's shoots are infested with overwintering larvae or if there is a history of serious infestation.

YELLOW APHIDS

The blackmargined aphid, Monellia caryella (Fitch), is found throughout the United States on pecan and certain other Carya species. It feeds mostly on the undersides of the leaves and prefers the primary and secondary veins. The summer form adults are parthenogenetic, and they produce live birth. They are easily recognized, as the wings are held flat over the body when the aphid is at rest and the outer edges of the forewings are colored black. The body is pale yellow and also edged with black. When these aphids are present in large numbers, the honeydew they excrete causes the foliage to become sticky and appear glossy. In humid climates, sooty mold subsequently grows on the honeydew, which gives the foliage a black sooty appearance. This black coating reduces the capacity of the leaves to manufacture starch, which reduces the vigor of the tree. Heavy feeding in late summer causes damage to the veins and sometimes leaflet shed. In the South there may be as many as 30 generations per year. This species is usually most abundant after midsummer.

A second yellow species, Monelliopsis nigropunctata (Granovsky) is found on the foliage of pecan and the other species of Carya in North America. It feeds almost entirely on the undersides of the leaflets on the tertiary veins at the point where these veins intersect larger veins. Feeding sites are therefore scattered across the leaflet blade. The summer form adults are parthenogenetic and give live birth. They are distinguished from the blackmargined aphid by the way they hold their wings when at rest. Also, the wings lack black margins, and only insignificant amounts of black occur on the body. The body is brighter yellow than that of the black margined aphid. This aphid produces about 60% of the honeydew that the blackmargined aphid produces, but the sooty mold effects are similar. Heavy feeding in the late summer causes damage to the veins at the point of feeding and sometimes leaflet shed. There may be as many as 32 generations annually. The aphid is usually most abundant in the spring but large populations also occur in late summer.

Control: Large aphid populations require chemical control, but indiscriminate use of pesticides kill predaceous insects, parasites and entomogenous fungi that help control aphids. In early season, controls should be applied when aphid numbers exceed an average of 20 aphids per compound leaf. In late season, this threshhold for control should be reduced to an average of 10 aphids per leaf.

BLACK PECAN APHID

The black pecan aphid, Tinocallis caryaefol (Davis), is considered more destructive than other aphid species because its feeding may cause defoliation in a short time. The first signs of feeding are the appearance of pale to bright-yellow rectangular areas on the leaflets; the color depends on the season and cultivar attacked. These yellow areas (up to one-fourth inch in diameter) eventually turn brown, and the entire leaf may drop prematurely. Black aphids feed on both sides of the leaflet and prefer the shaded, inner portion of the tree, but as injured leaflets drop, the aphids migrate toward the outside of the tree. Premature dropping of many leaves reduces the supply of food for the tree, prevents proper nut filling, and reduces the next year's bloom. Up to 26 successive generations occur through the summer, and each mature aphid produces about 40 young.

Control: Under certain conditions even small populations require chemical control because black pecan aphids can completely defoliate an orchard within 30 days. Controls should be applied when an average of one black aphid per compound leaf is found or their damage is seen frequently.

SPITTLEBUGS

The pecan spittlebug, Clastoptera achatina Germar, and the alder spittlebug, C. obtusa (Say), are common on pecan trees along the gulf coast, up the Atlantic coast from Florida to Massachusetts, and westward to Texas. They are prevalent in parts of Kentucky and Illinois.

Groups of young bugs (spittlebug nymphs) clustered together produce masses of white, foamy froth about the buds, tender shoots, and nut clusters. They are commonly found in sprin soon after the nuts have set and then appear again in midsummer. They suck the juices from tender growth, and heavy infestations kill the terminal shoots, resulting in a reduced crop.

Control: Large populations of spittlebugs require chemical control. Controls should be applied if 5 percent or more of the terminals have spittle masses. Light infestations generally do not cause enough damage to make control necessary.

LEAFMINERS

Leafminers, which are the larvae of certain moths, are among the smallest plant-feeding insects. They find both food and shelter in the thin space between the upper and lower surfaces of a single pecan leaflet. Each larva consumes only a small quantity of leaf as it develops, but the damage caused by excessive numbers and successive generations cannot be disregarded. Heavy infestations of these insects may defoliate pecan trees during late summer and fall. Although leafminers are widespread and have been observed in both the eastern and western United States on various species of hickory, walnut, and butternut, economically damaging infestations are not common.

A serpentine leafminer, *Nepticula juglandifoliella* Clemens is found wherever pecans are grown. The larvae confine their feeding to the chlorophyll containing cells just beneath the upper surface of the leaf, making a linear, or serpentine, mine about 2 inches long and one-twelfth inch wide, whitish to light tan in color, with a black line of frass running through the center.

Two other leafminers, *Cameraria caryaefoliella* (Clemens), which forms an upper-surface blotch mine, and *Phyllonorycter caryaealbella* (Chambers), which forms a lower-surface blotch mine, are also found on pecan. When the blotch mines are fresh, the separated leaf cuticle is a noticeable whitish color, commonly referred to as a frog eye.

Control: Light infestations of leafminers do not cause sufficient damage to warrant control. Apply controls when an average of 5 mines per leaf are observed. Insecticides used for aphids or hickory shuckworms will usually control these pests; however, excessive use of certain insecticides often cause leafminer outbreaks.

HICKORY SHUCKWORM

The hickory shuckworm, the larva of the oth *Laspeyresia caryana* (Fitch) is one of the ost destructive insects that infest the pecan. t is generally distributed throughout the ecan Belt from Georgia and South Carolina in the east through Texas in the west. Shuckworms also feed on hickory nuts and cause injury similar to that done to pecan. The shuckworm is primarily a nut infesting pest, but it is commonly found feeding in phylloxera galls on pecan in early spring.

Hickory shuckworms attack the nuts from about the first of June until harvest. From the time of first appearance until shell hardening late in August, these insects can continually destroy the interior of the nuts. Immature nuts infested early in the season fall to the ground. It is usually difficult to see the entry holes made by shuckworms except under magnification. Their presence, however, may often be detected in newly dropped nuts by a powdery white stain around the entry point. Much of the crop may be lost to shuckworms, especially when there is a light nut set.

After shell hardening, shuckworms tunnel in the green shucks and prevent the kernels from developing properly. Infested nuts may be poorly filled and may mature later than healthy nuts. Injured portions of the shucks stick to the nuts and interfere with processing, and the shells are often badly stained. Shuckworms pass the winter as full grown larvae in the shucks and emerge as moths the following spring.

Control: Growers with few trees and those not equipped to spray may reduce infestation by gathering and destroying pecan shucks at harvest. Plowing the shucks under in early spring may aid in control. The drops (small nuts) should be gathered and burned during midsummer. Proper insecticide application can reduce shuckworm populations to an insignificant level. Or 22-watt circline blacklight traps (2/acre) can be used to reduce shuckworm moth populations.

CURCULIOS

Conotrachelus hicoriae (Schoof), the so-called nut curculio, attacks several varieties of immature pecan nuts from late June through early August in some parts of Louisiana, Georgia, Arkansas, and Mississippi. The adult curculio deposits a single egg in the shuck of each nut during late June or early July. The puncture and the larval feeding within the shucks cause a bleeding of brown sap on the shuck and premature nut drop. Like the shuckworms, the creamy-white larvae continue to feed in the dropped nuts for about 2 weeks before leaving the nut. They form a pupal cell in the upper 2 to 4 inches of the soil. The adults emerge from August to October. The insect produces but one generation a year.

Control: When trees have a good nut crop, *C. hicoriae* damage may go unnoticed or be attributed to hickory shuckworms. Chemical spray may be necessary when jarring the tree indicates the presence of many adults.

STINK BUGS AND OTHER PLANT BUGS

The southern green stink bug, *Nezara viridula* (L.), the leaffooted bug, *Leptoglossus phyllopus* (L.), and similar sucking insects cause black pit and kernel spot of pecan nuts. Darkened insides of immature nuts, known as black pit, often indicate stink bug feeding before shell hardening. This feeding causes premature dropping. Brown or black stains sometimes develop on the shuck at the puncture site, and soon after the nuts drop, these spread over the entire shuck surface. Stink bug punctures occurring after shell hardening do not cause nut drop. However, black to brown spots from one-sixteenth to three-sixteenths inch in diameter that form a pithy, porous area known as kernel spot are seen after shelling. The spots produce a localized bitter taste that does not extend to the rest of the kernel. The severity of damage varies with the number of plant bugs in a grove. The abundance of bugs depends on the presence of the native plants or cover crops on which they breed or adjacent agronomic crops.

Control: The avoidance of summer legumes such as cowpeas, soybeans, and peanuts and of garden crops such as okra, beans, pumpkins, squash, and tomatoes near pecan groves will help control plant bugs.

PECAN WEEVIL

Pecan weevils, *Curculio caryae* (Horn), cause two kinds of nut damage depending on the stage of nut development at the time of attack.

The first damage is caused by adult weevils feeding on kernels in the water stage, before shell hardening. This feeding generally results in a drop of all punctured nuts, but the infestation may pass unnoticed because other insects and factors can also cause a premature nut drop. Weevil-punctured nuts can be identified by a tobacco juicelike stain around the feeding site. Dark patches develop on the nut surface, and in a few days the nuts drop from the trees.

The second kind of damage is caused by weevil grubs, or larvae, feeding in the partially matured nuts. Damaged mature nuts bleed little and do not drop prematurely; in fact a high percentage will not fall at harvest since the shucks do not open at maturity. The grubs feed on the kernels for several weeks. When fully grown, about three-fifths inch long, the creamy-white grubs with reddish-brown heads leave the nut through circular holes about one-eighth inch in diameter. These larvae enter the soil where they remain for 2 or 3 years before emerging as adults. Infested nuts are worthless since the larvae normally destroy the kernels, and the shucks often adhere to the shell. This damage is noticeable at harvest time. Practically the entire crop may be destroyed in seasons when large numbers of weevils are present. Few insects match or surpass it as a pest of pecan or hickory.

Control: The timing of weevil spray is determined by the appearance of the adults, usually during late summer, August-September. Growers not prepared to spray and those with dooryard trees can reduce weevil injury by placing sheets under trees and lightly jarring the limbs to shake weevils free. The weevils can then be collected and killed.

MITES

Several speices of mites attack pecan trees throughout the Pecan Belt. The most common and injurious mite is known only by its scientific name, *Eotetranychus hicoriae* (McGregor), but it is somethimes referred to as the pecan leaf-scorch mite. Heavy infestations of this mite cause serious foliage loss. The mite is pale green and barely visible to the naked eye. It feeds primarily on the undersides of the leaves, but occasionally may be found on the upper sides.

Affected leaflets show a slight discoloration between the veins near the midribs where the mites usually begin feeding. Later, the discoloration spreads outward, and the leaflets appear scorched. Severe scorch symptoms are dark-brown or liver-colored blotches that later develop into dead areas of irregular size and pattern. Severely injured leaflets turn brown and drop off. Infestation generally starts on the lower branches of pecan trees and spreads upward. Injury has been observed in June, but is usually more severe from late summer to fros The mites develop rapidly in hot dry weather and produce numerous generations each year.

Control: Treatment for mites can be combined with that for aphids and with that for diseases since they are needed at or near the same time.

FALL WEBWORM

Fall webworms, the larvae of the moth *Hyphantria cunea* (Drury), feed in colonies and produce large dirty-white webs on the terminal branches of pecan trees in late summer and fall. These caterpillars hatch from a mass of greenish-white eggs deposited on a leaf by a single moth. They feed on both surfaces of the leaves and enlarge the web as they spread.

The fully grown caterpillars, about 1 inch long, are covered with long white and black hairs. They spin flimsy hairy cocoons beneath loose debris near the surface of the soil. The adult moths have a wingspan of about 1 inch, are usually white, and sometimes have a few black or brown spots on the forewings. Usually there are two broods a year, the second feeding late in the summer and in the fall. The insect overwinters as a pupa, and moths appear during the following year in April or May.

Control: Control is usually only necessary when the insects are numerous in a grove, but any chemical insecticides should be applied when the caterpillars are small. It may be practical to mechanically remove the webs of small populations from the trees before the caterpillars have left them and preferably before they have done much feeding.

WALNUT CATERPILLAR

Walnut caterpillars, the larvae of the moth *Datana integerrima* Grote & Robinson, feed in groups that often eat all the leaves on small pecan trees or on individual limbs of large trees; however, they do not form webs on the leaves. The immature larvae are reddish brown and have narrow cream-colored lines that extend the length of the body. The full-grown caterpillars are black, nearly 2 inches long, and thickly covered with long dirty-white or grayish hairs.

In southern regions the first generation appears in June and July, and the second generation in late August and September. The walnut caterpillar is found in pecan producing areas east of the 100th meridian; west Texas, Arizona, and New Mexico are currently free of this pest.

Control: Spray treatments similar to those recommended for the fall webworm will control this insect. Caterpillars clustered on the trunk or limbs of a tree may be destroyed by crushing or burning.

PINHOLE AND SHOTHOLE BORERS

Several similar insect species attack weak pecan trees. Some feed only on the bark and in the cambium region; others burrow deep into the heartwood. Occasionally they attack healthy trees, but they rarely cause serious damage since the larvae cannot subsist on wood with a good sap flow. Severe drought, mechanical damage, or cold injury often weaken trees for borer attack.

The so-called pinhole borers or scolytid ambrosia beetles, *Xyleborus affinis* Eichhoff, *X. ferrugineus* (Fab.), and *X. saxeseni* (Ratzeburg), which inhabit the trunks and stems of many hardwood trees in the southeastern United States, also damage pecan trees. These scolytid beetles infest all sizes of pecan trees ranging from 1-year-old nursery trees to 50-year-old trees in commercial plantings. The adults are small brown to reddish-brown elongate beetles with compact cylindrical bodies about one-tenth inch long. The beetles bore holes one-sixteenth to one-thirty-second inch in diameter in the pecan stem and lay their eggs in the sapwood. The entrance holes give the tree trunk or stem the appearance of having been hit by shot. As the beetles construct the galleries, they push the sawdust-like borings to the outside through the entrance hole. The white C-shaped grubs feed upon fungi growing in the brood cells constructed by the beetles. The associated fungi often give pecan wood a blueish-black stain.

Control: To control the borers, maintain healthy trees by good fertilization and watering practices, reduce sources of infestation, such as dead wood and prunings, and control winter injury by wrapping and planting the proper cultivars.

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Pesticides used improperly can be injurious to man, animals, and plants. Follow the directions and heed all precautions on the labels.

Store pesticides in original containers under lock and key--out of the reach of children and animals--and away from food and feed.

Apply pesticides so that they do not endanger humans, livestock, crops, beneficial insects, fish, and wildlife. Do not apply pesticides when there is danger of drift, when honey bees or other pollinating insects are visiting plants, or in ways that may contaminate water or leave illegal residues.

Avoid prolonged inhalation of pesticide sprays or dusts; wear protective clothing and equipment if specified on the container.

If your hands become contaminated with a pesticide, do not eat or drink until you have washed. In case a pesticide is swallowed or gets in the eyes, follow the first-aid treatment given on the label, and get prompt medical attention. If a pesticide is spilled on your skin or clothing, remove clothing immediately and wash skin thoroughly.

Do not clean spray equipment or dump excess spray material near ponds, streams, or wells. Because it is difficult to remove all traces of herbicides from equipment, do not use the same equipment for insecticides or fungicides that you use for herbicides.

Dispose of empty pesticide containers promptly. Have them buried at a sanitary land-fill dump, or crush and bury them in a level, isolated place.

NOTE: Some States have restrictions on the use of certain pesticides. Check your State and local regulations. Also, because registrations of pesticides are under constant review by the Federal Environmental Protection Agency, consult your county agricultural agent or State extension specialist to be sure the intended use is still registered.

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U.S. Department of Agriculture, Forest Service.
1979. Walnut insects and diseases. Workshop Proc.
U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-52,
100 p. U.S. Dep. Agric. For. Serv., North Cent.
For. Exp. Stn., St. Paul, MN.

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MACRONUTRIENT DEFICIENCY SYMPTOMS IN SEEDLINGS OF FOUR NORTHERN HARDWOODS

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Presently very little is known about the inorganic nutrient requirements of our important orthern hardwood species. Little information oncerning optimum nutrient levels, critical anges for essential elements, visual deficiency mptoms, and physiological effects of nutrient eficiencies has been published.

Detecting deficiencies is essential if timely cor- ctive action is to be undertaken. A visual foliar mptom approach is rapid, inexpensive, and reli- le as leaves are especially sensitive indicators of ficiencies (Kramer and Kozlowski 1960). How- er, before any corrective action is taken, supple- ntal chemical analyses of foliar tissue should be ade to verify suspected nutrient deficiencies hares and Finn 1972).

eficiency symptoms for some hardwoods have b n described: basswood (Ashby 1959, Ashby and ka 1959); pin oak (Hacskaylo and Struthers 1 59); locust and sweetgum (Hacskaylo 1960); A erican elm, box elder, hackberry, Russian ol e, and silver maple (Sucoff 1961, Perala and S off 1965, Lamb and Murphy 1968); eastern cot- to wood (Hacskaylo and Vimmerstedt 1967); yel- lo -poplar (Ike 1968); black locust, black walnut, ea ern cottonwood and pin oak (Hacskaylo *et al.* 199); black walnut (Phares and Finn 1972); red m le, gray birch, and black cherry (Walker 19); and red maple (Smith 1976). Except for As by, Walker, and Smith, little information is av lable on the effects of deficiencies on the gr th of northern hardwood species.

veral related studies have dealt with potas- siu deficiencies in American elm (Perala and Su ff 1965), effects of macronutrient and molyb- de m deficiencies on yellow birch growth and nutrient uptake (LaFlamme and Lafond 1967, Hoyle 1971, and Hannah 1973), effects of various levels of N, P, and K on paper birch growth (Bjorkbom 1973), the relation of nitrogen deficiencies to sugar maple decline (Mader *et al.* 1969), and the effect of Mn and Cu on P uptake in sugar maple (Gysi *et al.* 1975).

Our studies were established to observe, photograph, and report distinctive visual deficiency symptoms for the macronutrient elements (N, P, K, Ca, Mg, and S) in sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.), and paper birch (*Betula papyrifera* Marsh.) seedlings. Deficiency symptoms illustrated in this paper together with supporting foliar analyses and growth data are presented as preliminary guides in diagnosing nutritional disorders of these seedlings grown under nursery, greenhouse, and laboratory conditions.

The chemical composition and ovendry weights of foliage, stems, and roots of seedlings grown in complete single element deficiency solutions and distilled water were compared. Seedling height growth and the number of leaves produced per seedling under the various treatments were also compared.

METHODS

Sand culture nutrient deficiency studies with young sugar maple, red maple, paper birch, and white ash seedlings were conducted in the Forestry Sciences Laboratory greenhouse at Marquette, Michigan. The maples were studied in the summer of 1972; the ash and birch were studied in the summer of 1973.

Sugar maple seeds with protruding radicles and emerging red maples in the cotyledon stage were gathered, rinsed thoroughly with distilled water, and planted directly in pots. Paper birch seeds were germinated in distilled water in petri dishes under fluorescent light until cotyledons expanded. The radical end of white ash seed, which was difficult to germinate, was clipped to promote uniform germination. After clipping, the seeds were placed on damp filter paper in petri dishes until seeds with elongating radicles were available for planting.

Two to three germinants were planted in 660 grams of high-grade silica sand in 550 cm^3 clay pots lined with inert, clear, polyethylene bags. Pin holes were pricked into the plastic bags through the basal hole of the clay pot for bottom drainage. The sand in the 1973 birch and ash trials was leached with 20 percent cold hydrochloric acid (for 3 days followed by washing with distilled water until there was no change in pH of the standing water); unleached sand was used in the earlier 1972 maple trials. The improved procedure in 1973 was thought necessary to produce Fe deficiency symptoms[1] and a better procedure for producing Ca deficiency symptoms with the high-grade silica sand.

Germinants were grown in distilled water and then conditioned in gradually strengthened complete nutrient solutions for 46, 25, 65, and 33 days for sugar maple, red maple, paper birch, and white ash, respectively. Seedlings in each pot were thinned to leave the most vigorous individual.

Following the development of the first true leaves, the seedlings were given a complete nutrient plus Fe-EDTA solution (Hacskaylo 1960) until 120 ml of full strength solution per pot was accumulated and retained by capillary action. At the end of the conditioning period the pots were flushed with 150 ml of distilled water and the deficiency treatments were begun. Thereafter pots were reflushed with distilled H_2O and replenished with appropriate fresh nutrient solutions at 2-week intervals.

Cultural solutions were complete except fo omission of one of six elements: N, P, K, Ca, M S. Treatments also included controls: one wit complete nutrient solution, and one with dist water only. Controls were used as checks on tamination and to provide a basis for jud growth responses after deficiency treatments applied. Solutions were prepared with rea grade or high purity chemicals and pyrex- distilled water (See Appendix, table 25 and 2 composition, substitutions, and strength of th lutions used). Cultural solution pH values us the pots ranged from 4.8 to 5.5 and were 5.8 fo distilled water. Watering and flushing kep values above pH 5.0 in all treatments. Mois losses were monitored with weighed represe tive pots and replaced once or twice daily distilled water. Nutrient status in the pots maintained by adding 10 ml of cultural solu once each week and completely flushing an plenishing with new nutrient solution every weeks. Injurious surface concentrations of s formed by rapid evaporation of cultural solut added from above during hot weather (He 1966), were avoided by top watering, breakin surface crusts weekly, and biweekly flush Maples were grown in deficient cultural solut for 117 days; ash and birch for 113 days.

A randomized block design with 5 replicatio the 6 deficiency and 2 control treatments was for each species. Individual potted seedl within each replication were the experime units to which treatments were randomly app Each replication was formed by selecting s lings of uniform heights. There were two comp nutrient controls in each birch and ash repli but only one for the maples.

Plants were grown under at least a 16-h photoperiod with supplemental fluorescent an candescent lighting of 200- to 300-foot candle the leaf surface. The greenhouse was covered a shade cloth to reduce normal daylight inten by 50 percent and to lower summer greenh temperatures. Day temperatures were kept be 34C and night temperatures above 12C. Ins were controlled by hand. Pots within replicat and entire replications were rotated twice wee to equalize bench and lighting effects.

Visual deficiency symptoms were describe they appeared, followed at weekly interv hroughout their development, and photographed t significant stages. Symptoms included unusual olor, necrosis, wilting, distortions; general size nd growth of leaves, petioles, buds, and stems. lso noted were changes in color of interveinal reas, veins, bases, margins, and tips of young and ld leaves. Types of necrosis in leaves included: arginal scorch, tip scorch, salting, spotting, and lotching. "Salting" refers to grain-sized spots of alt; "spotting" to pinhead-sized spots; and blotching" to individual, usually irregularly- haped areas larger than spots which became nec- tic all at once. Significant growth reductions in edling height growth and in ovendry weights of mponent parts as compared to the complete nu- ient controls were also considered diagnostic of a vere nutrient deficiency.

---

[1] *Results of the iron deficiency trials are not reported here because although visual symptoms developed they could not be confirmed by the nutrient concentration percentages and there was no growth retardation in the paper birch or white ash seedlings.*

Seedling height growth was measured at 2-week itervals. At completion of the study, leaves were cunted and plants were separated into leaves, sms, and roots. Chemical analyses of these compnents were made on composited samples from t five replications, ovendried at 70C, and ground ia Wiley[2] mill to pass a 20-mesh screen. Various sges of deficiency symptoms and leaf maturity a represented in the analyzed material. Total nrogen was determined by the semimicro-Kjeldal method (Bremner 1965); total S was by nitric pchloric acid digestion (Tabatabai and Bremner 10); and P, K, Ca, Mg, Fe, Al, Cu, Zn, B, and Mn by emission spectrography of dry-ashed (485C for 4 o 5 hours) samples.[3] Checks with duplicate saples proved to be satisfactory.

reatment effects on seedling growth, weight, an size were evaluated with an analysis of variane and Duncan's New Multiple Range test. Composting samples to obtain sufficient material for chnical analyses ruled out statistical tests of the inflence of treatments on nutrient content.

Spplemental laboratory studies were run in theummer of 1975 to get better quality photos for P ad K in sugar maple and P and S in white ash seeings.

VISUAL DEFICIENCY SYMPTOMS, EFFECTS ON GROWTH AND CHEMICAL COMPOSITION OF SEEDLINGS

Visual foliar symptoms of nutrient deficiencies are described separately for each species because symptoms for a given element often varied markedly among species. This approach should make it easier to pinpoint deficiencies within a species. Color photographs illustrate plants exhibiting distinguishing foliar symptoms and advanced stages of each deficiency.

Seedlings grown in complete nutrient solutions were healthy plants with normal leaves (figs. 1A, 2A, 3A, 4A). Their foliage was dark green except for white ash which varied from green to dark green. Expanding apical leaves on all species normally were light colored or reddish. These colors were not indicative of deficiencies.

All seedlings grown in distilled water without nutrients were stunted and had small yellow-green, yellow, or red foliage and petioles (figs. 1B, 2B, 3B, 4B). Height growth on sugar maple and red maple seedlings ceased immediately after they were put in distilled water cultures, while white ashes and paper birches stopped growing after 14 and 21 days, respectively. Foliage on distilled water seedlings was borne at abnormal angles to the stem.

Besides foliar symptoms, many deficiencies caused obvious growth reductions and other effects on the above-ground parts of seedlings. These growth losses often occurred before any visual foliar symptoms appeared, particularly in the cases of nitrogen, phosphorus, or calcium deficiencies. As with visual foliar symptoms, the impact of a certain nutrient deficiency on growth often differed among species.

The effect deficiencies had on height growth varied with species. The height growth of white ash and sugar maple seedlings was not as greatly affected by deficiencies because they stopped growing soon after treatments were begun. Paper birch and red maple seedlings, on the other hand, continued growing longer, allowing more time for the deficiencies to influence growth. (Only statistically significant effects of seedling growth responses are given in this section (tables 1-24).

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[2] *ention of trade names does not constitute encrsement of the products by the USDA Forest Serice.*

[3] *hemical analysis were made by the Research Anytical Laboratory, Department of Soil Science, Unersity of Minnesota.*

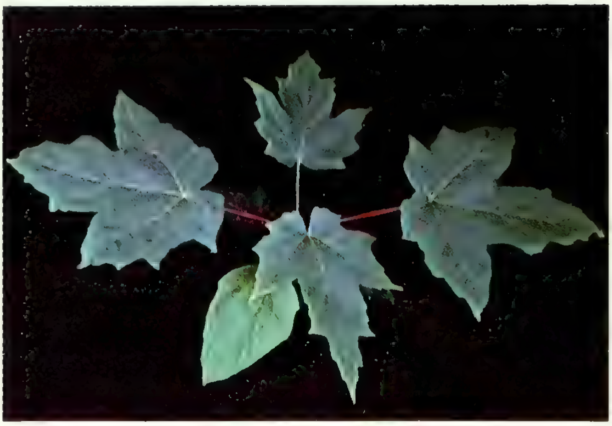


Figure 1A.—*Sugar maple complete nutrient control.*

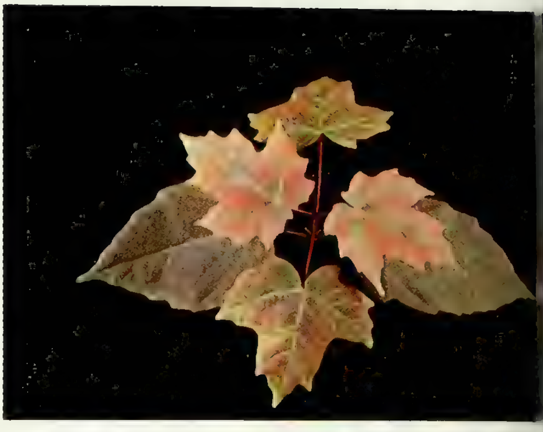


Figure 1B.—*Sugar maple distilled water co*

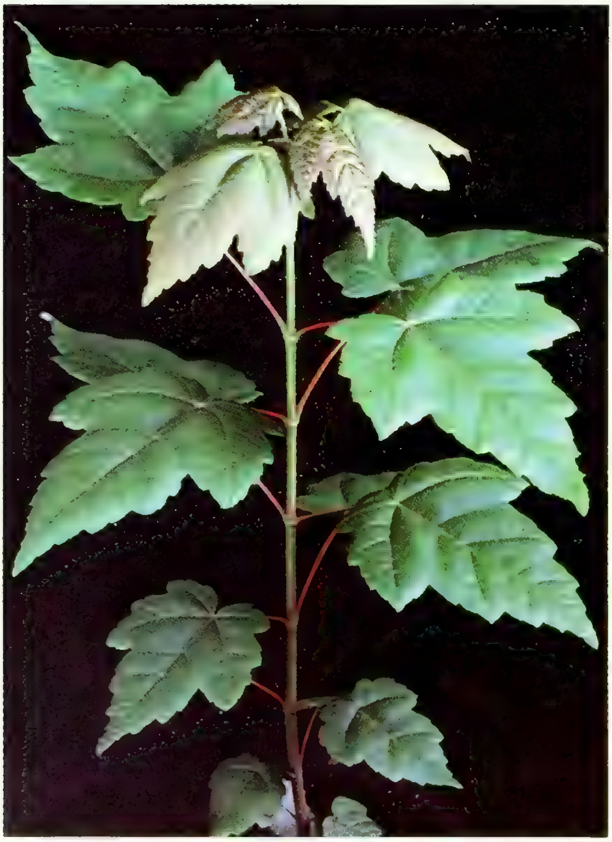


Figure 2A.—*Red maple complete nutrient control.*

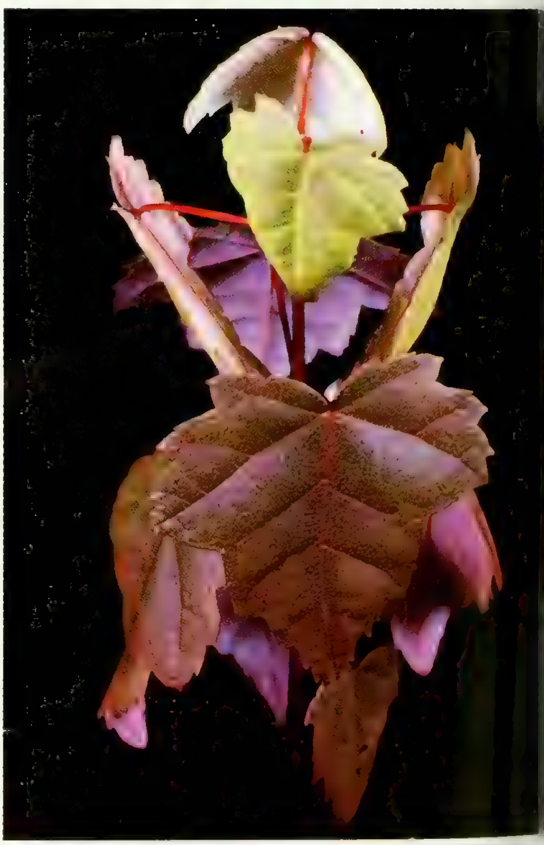
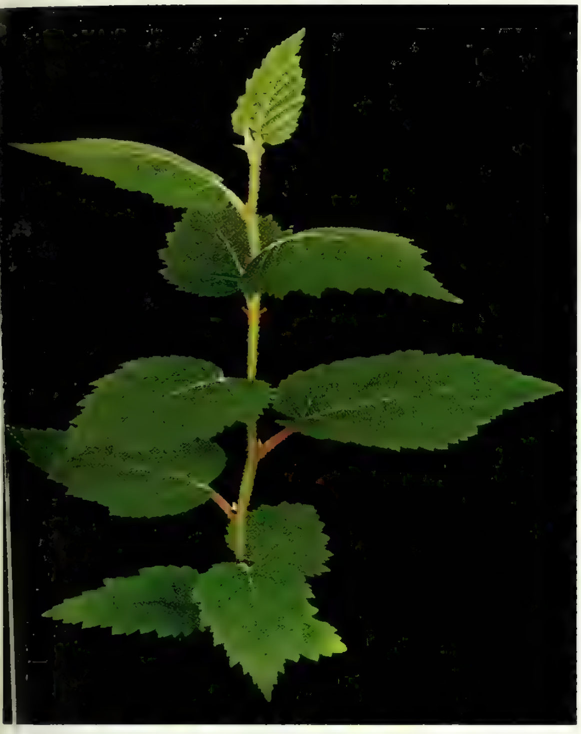


Figure 2B.—*Red maple distilled water contr*



F ure 3A.—*Paper birch complete nutrient control.*

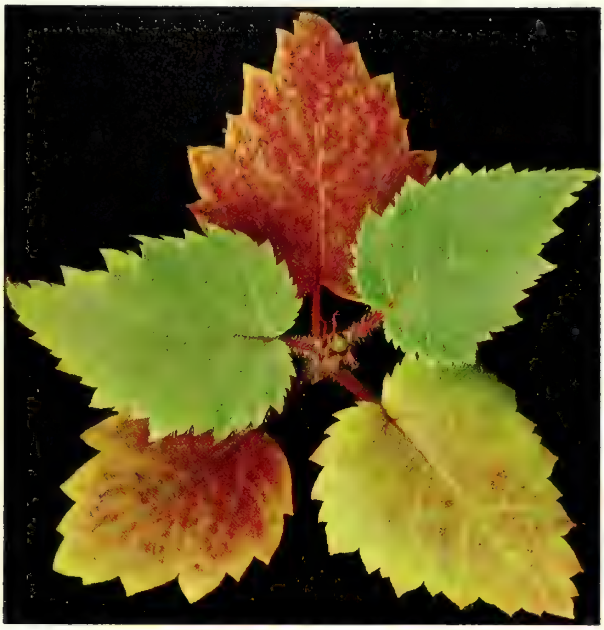


Figure 3B.—*Paper birch distilled water control.*

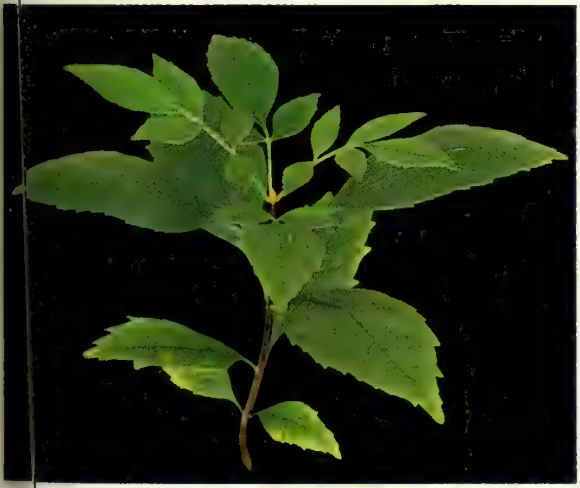


Fig re 4A.—*White ash complete nutrient control.*

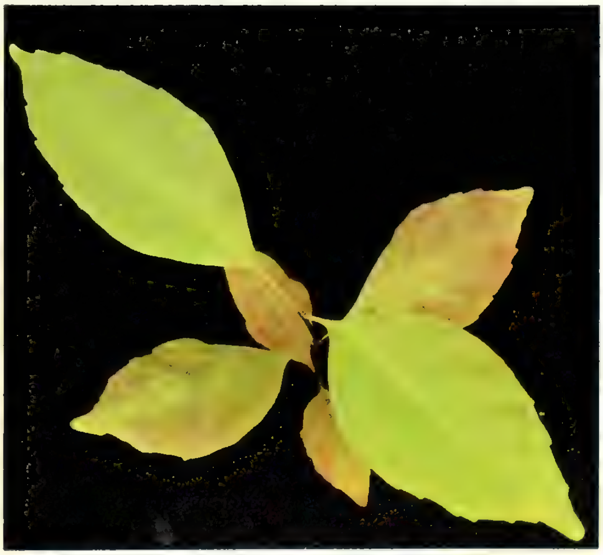
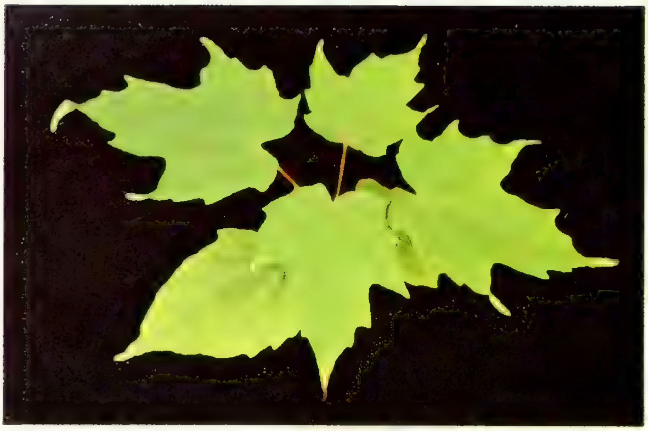
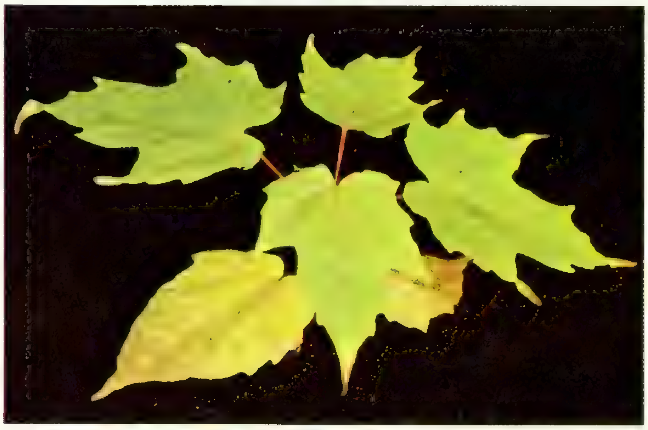


Figure 4B.—*White ash distilled water control.*

C emical analysis of seedling parts verified the defi encies, while the data provide a guide to the ma itude of the differences that can be expected bet en abnormal and healthy seedlings elsewhere. Nutrient content in stems, roots, and all foliage of seedlings is expressed as the percent composition (concentration) and the total weight (total or absolute amount) of the element taken up.





Distinguishing symptoms (top), advanced symptoms (bottom) in sugar maple.

SUGAR MAPLE

Nitrogen

Deficiency symptoms

Initially, entire leaf surfaces throughout the plant gradually changed from dark green to light green. Some leaf lobe tips turned yellow and subsequently scorched. After this the lower part of leaves turned completely yellow to contrast distinctly with light-green upper leaves. In advanced stages this yellowing in lower leaves was followed by more necrotic tip and marginal scorching and extensive blotching which gradually progressed up the stem.

Growth

Shoot elongation almost stopped as soon as seedlings were switched from complete to N-deficient cultural solution. As a result, they appeared stunted and had fewer and smaller leaves than complete nutrient control seedlings. Omitting N caused significant losses in total seedling dry weight (table 1) and all component parts (foliage, stem, roots) of it. N-deficient seedlings weighed 74 percent less than the complete nutrient controls and were comparable to the distilled water controls except root weights were greater for N-deficient seedlings.

Nutrient content

Total uptake in deficient seedlings was a fifth of that in complete controls. Concentrations in various deficient seedling tissues fell to near 1 percent (table 1).

Table 1.— *Average height growth, ovendry seedling weight, nitrogen concentrations and total content in component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

			Nitrogen						
			Concentration			Total Content			
Solution	**Height growth**[2]	**Dry weight**[3]	**Leaves**	**Stem**	**Roots**	**Leaves**	**Stem**	**Roots**	**P**
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	27.4	4.32	2.24	1.88	1.83	32.70	8.27	44.29	8
Deficient	3.0	1.73	0.82	1.20	1.17	3.20	2.16	13.57	1
Water	2.2	1.04	0.43	–[4]	0.17	1.85	–	3.55	

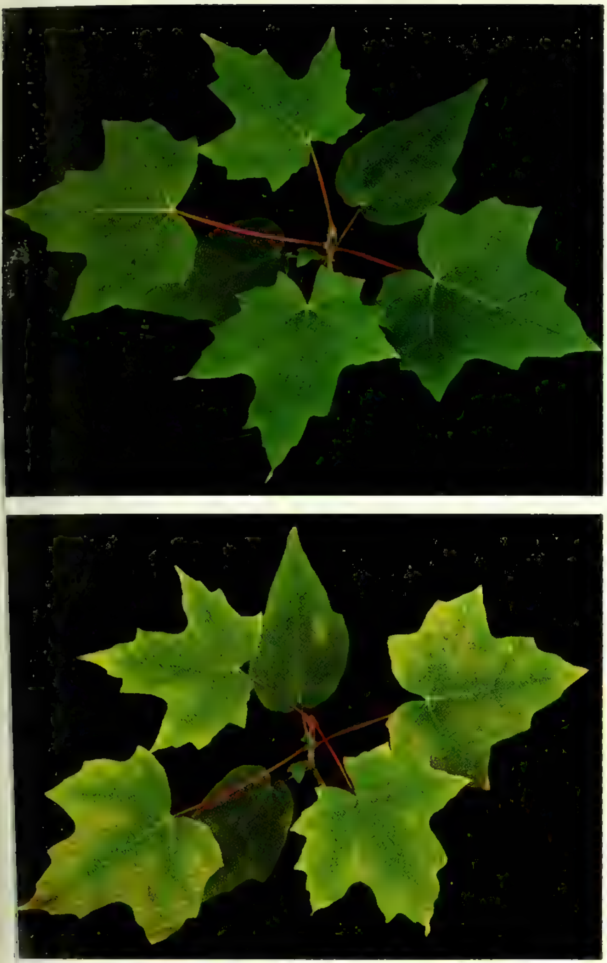
[1] See Appendix table 28 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.

[4] Dashes indicate that inadequate material was available for chemical analysis.

Phosphorus



Distinguishing symptoms (top), advanced mptoms (bottom) in sugar maple.

Deficiency symptoms

First, all leaves throughout the plant quickly developed distinctive dull dark-green surfaces; light-green and yellow-green mottles and necrotic tips showed up shortly thereafter. Later the mottles became yellow and necrosis spread along the leaf margins. Finally, discolored, water-soaked-appearing spots developed on interveinal tissues of the lower leaves. These spots enlarged and rapidly coalesced into larger blotches. Spotting symptoms progressed upward from the lower leaves.

Growth

Phosphorus, like N, was crucial to growth; its omission caused stunting and fewer leaves were produced. All aspects of seedling growth were comparable to growth of the distilled water controls.

Nutrient content

P-deficient seedlings took up 9 times less P and concentrations were a third of normal (table 2).

Tble 2.—*Average height growth, ovendry seedling weight, phosphorus concentrations and total content in component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

			Phosphorus						
			Concentration			Total Content			
Slution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Coplete	27.4	4.32	0.16	0.24	0.24	2.34	1.06	5.81	9.21
Decient	3.2	1.46	0.05	0.09	0.07	0.22	0.16	0.59	0.97
Wer	2.2	1.04	0.05	0.09	0.10	0.22	0.10	0.50	0.82

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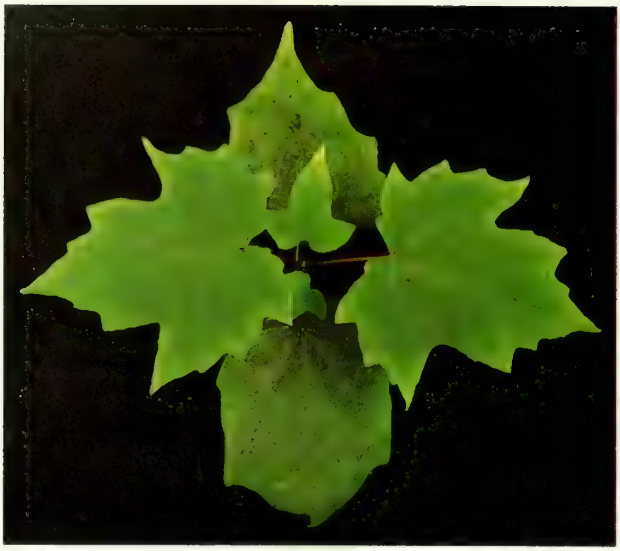
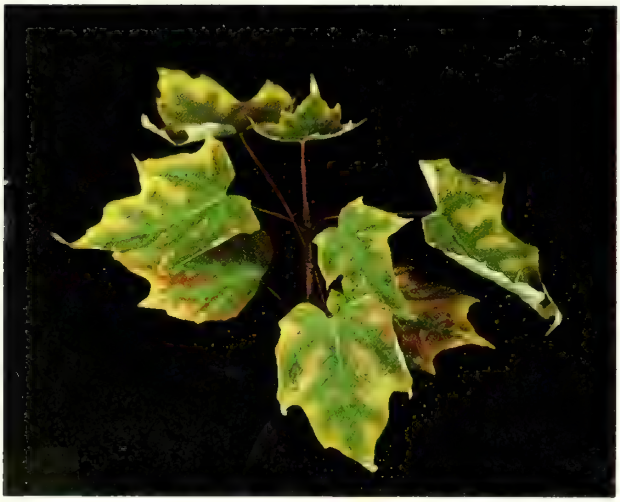
[1] e Appendix table 28 for more complete growth data.
[2] ight growth from treatment establishment until harvest.
[3] endry weight of entire plant.





Distinguishing symptoms (top), advanced symptoms (bottom) in sugar maple.

Potassium

Deficiency symptoms

Yellow leaf tips, petiole drooping, and necrotic spotting were the earliest signs of K-deficiency. Symptoms developed slowly, beginning with lower leaf margins turning yellow green and then gradually yellow. Yellowing widened inward between the green midrib and main veins, giving the remaining green tissues the appearance of a deeply lobed white oak leaf. Similar symptoms appeared later in upper leaves, but the green-patterned edge was fringed with a purple tint. Finally, yellow areas bronzed or scorched and leaf margins curled up. Leaf petioles were also purple. Dead leaves remained attached to the stem.

Growth

Dry weight for all component parts were reduced by omitting K, but stem and root weights were reduced more than foliage weights. Yields in both stems and roots in K-deficient seedlings were comparable to those in the distilled water controls.

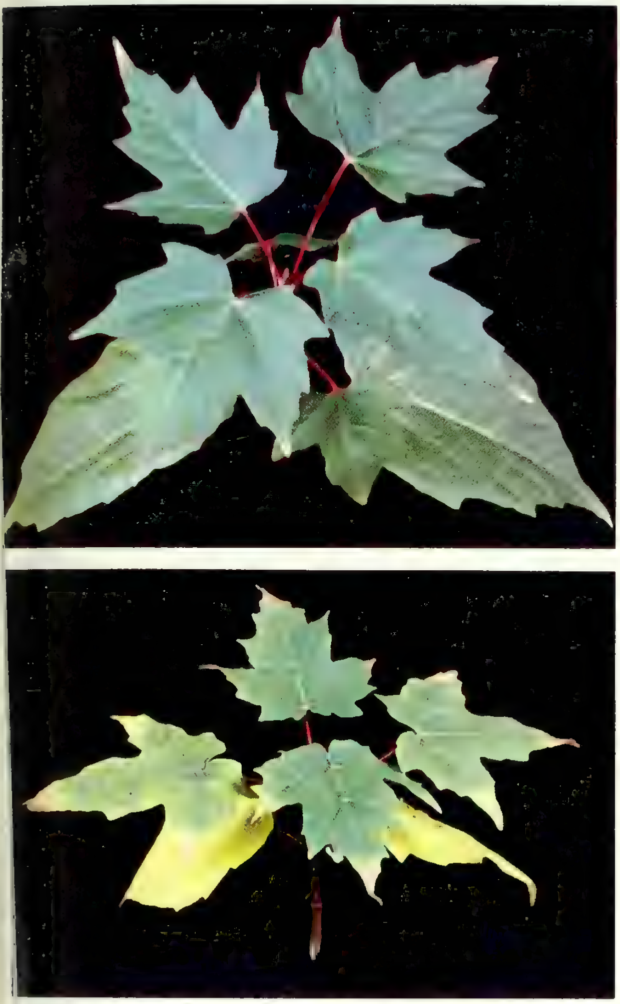
Nutrient content

Deficient seedlings showed 8 times less uptake and lower concentrations of K, especially in the leaves and roots, than normal seedlings (table 3).

Table 3.—*Average height growth, ovendry seedling weight, potassium concentrations and total content component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

Solution	Height growth[2]	Dry weight[3]	Potassium						
			Concentration			Total Content			
			Leaves	Stem	Roots	Leaves	Stem	Roots	Pla
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	27.4	4.32	0.90	0.57	0.94	13.14	2.51	22.75	38.4
Deficient	10.6	1.65	0.23	0.33	0.34	1.96	0.59	2.11	4.6
Water	2.2	1.04	0.23	0.48	0.41	0.99	0.53	2.05	3.5

[1] See Appendix table 28 for more complete growth data.
[2] Height growth from treatment establishment until harvest.
[3] Ovendry weight of entire plant.



Distinguishing symptoms (top), advanced mptoms (bottom) in sugar maple.

Calcium

Deficiency symptoms

Newly formed upper leaves were greatly reduced in size by Ca deficiency. Overall fading from light- to yellow-green occurred first in upper leaves and then in lower leaves. Yellowing began simultaneously in all upper leaf tips and progressed inward toward the leaf base. Yellow leaf tips turned bright red before dying while the rest of the leaf remained yellow green. In more advanced stages, the first or lowest pair of true leaves turned yellow before drying and rolling up.

Growth

Leaf number and all other aspects of seedling growth were greatly diminished by the lack of Ca. Calcium-deficient seedlings were similar to the distilled water control seedlings and weighed less than those grown under other deficiency treatments. Calcium-deficient seedlings were about 72 percent lighter than the controls.

Nutrient content

Almost twelve times more Ca was taken up by normal seedlings than those grown without Ca (table 4). Foliar and stem concentrations indicated only a threefold difference and root concentrations were lower.

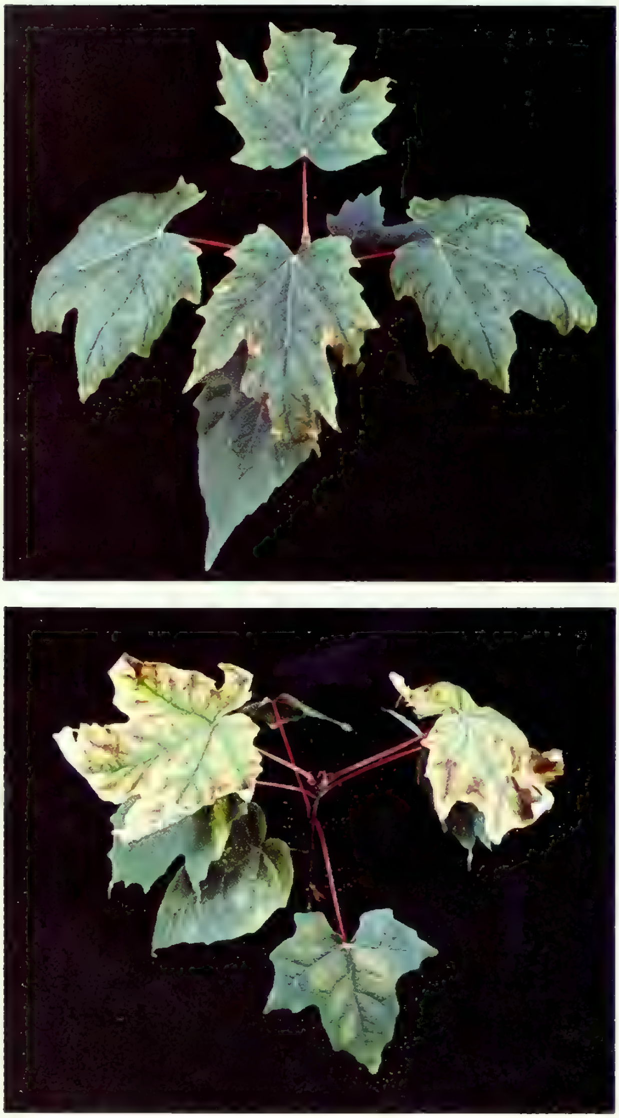
able 4.—*Average height growth, ovendry seedling weight, calcium concentrations and total content in component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

			Calcium						
			Concentration			Total Content			
Slution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Cmplete	27.4	4.32	2.38	1.43	0.76	34.75	6.29	18.39	59.43
Dicient	4.6	1.23	0.86	0.42	0.10	3.96	0.67	0.61	5.22
Wter	2.2	1.04	0.97	0.84	0.22	4.17	0.92	1.10	6.19

ee Appendix table 28 for more complete growth data.

eight growth from treatment establishment until harvest.

vendry weight of entire plant.



Distinguishing symptoms (top), advanced symptoms (bottom) in sugar maple.

Magnesium

Deficiency symptoms

The upper leaves developed a distinctive attern: interveinal tissues turned light green ile midribs, main veins, and adjacent tissue remained dark green. Leaf tip and edge yello ng and scorch also accompanied this symptom. L t-green mottles and yellow-green patches bega ppearing on lower leaves next, but the distin ve margin-to-rib pattern did not develop. Necros in old leaves consisted of scattered salting and tting. In young leaves necrosis finally expa ed down between the main veins, and the dried af tips curled down.

Growth

Dry weights of component parts of Mg-defic nt seedlings declined, but seedling height gro h, leaf numbers, and leaf size were not greatl ffected by this deficiency.

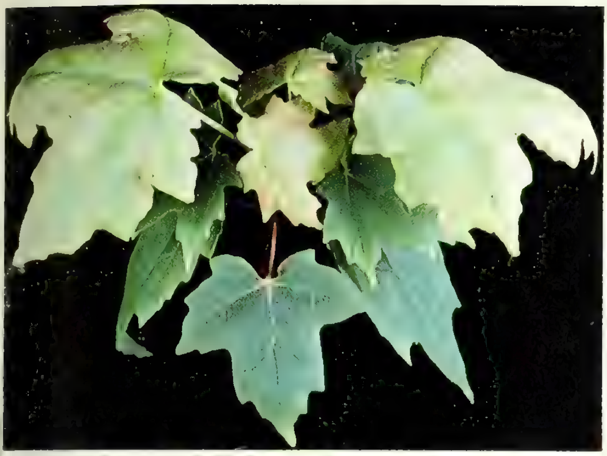
Nutrient content

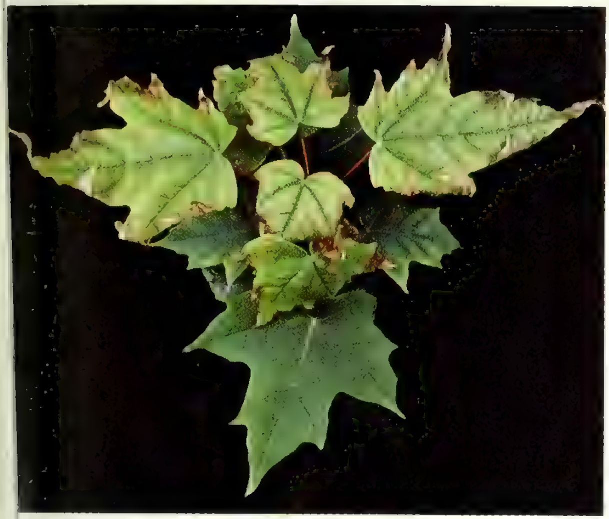
Total uptake by deficient seedlings was n ch lower (10 times), especially in the roots (16 ti s) than complete control seedlings (table 5).

Table 5.—*Average height growth, ovendry seedling weight, magnesium concentrations and total conten component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled w solutions for 117 days*[1]

			Magnesium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Pla
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	27.4	4.32	0.43	0.16	0.30	6.28	0.70	7.26	14.
Deficient	17.4	1.74	0.09	0.06	0.07	0.80	0.11	0.46	1.
Water	2.2	1.04	0.20	0.08	0.06	0.86	0.09	0.30	1.

[1] See Appendix table 28 for more complete growth data.
[2] Height growth from treatment establishment until harvest.
[3] Ovendry weight of entire plant.





Distinguishing symptoms (top), advanced ymptoms (bottom) in sugar maple.

Sulfur

Deficiency symptoms

First signs of S deficiency appeared on new upper foliage. These leaves were light green with a pinkish cast, cupped downward and curled, and had scorched tips; later they turned yellow green and developed scorched margins. Lower leaves remained dark green at first, then gradually lightened to a uniform yellow-green color with necrotic tips and interveinal blotches.

Growth

Sulfur deficiency caused a moderate reduction in seedling height growth. Weights of deficient seedlings parts were significantly below those of the complete nutrient controls but yet almost twice as heavy as the distilled water controls.

Nutrient content

Sulfur uptake was reduced about sixfold for the various seedling parts (table 6).

able 6.—*Average height growth, ovendry seedling weight, sulfur concentrations and total content in component parts of sugar maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

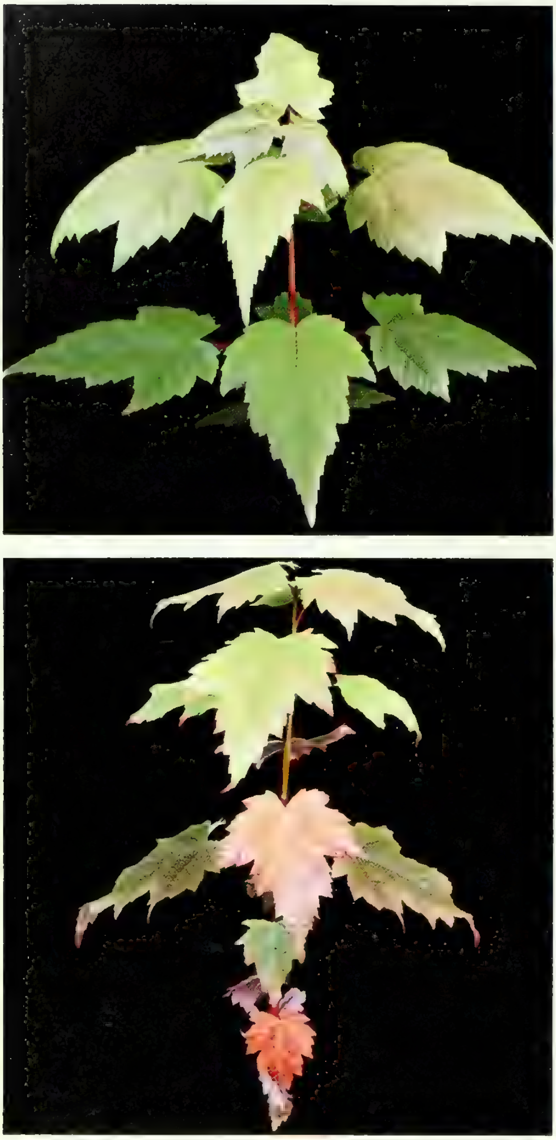
			Sulfur						
			Concentration			Total Content			
Slution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Cmplete	27.4	4.32	0.19	0.15	0.26	2.77	0.66	6.29	9.72
Dficient	8.6	2.26	0.07	0.06	0.07	0.49	0.14	0.92	1.55
Wter	2.2	1.04	–[4]	–	–	–	–	–	–

See Appendix table 28 for more complete growth data.

Height growth from treatment establishment until harvest.

Ovendry weight of entire plant.

Dashes indicate that inadequate material was available for chemical analysis.



RED MAPLE

Nitrogen

Deficiency symptoms

Nitrogen deficiency first showed up as a grad fading of the lower leaves from green to ligh green in red maple seedlings. This fading sy tom gradually progressed up the stem to the up foliage. In more advanced stages the lower foli turned pink, then red, and the basal lea scorched on the tip, turned brown, rolled up, finally abscised.

Growth

N-deficient seedlings weighed about half much as the complete nutrient controls; most the weight loss occurred in the foliage and ro Newly formed leaves stayed noticeably smal than older leaves as the deficiency developed.

Nutrient content

Total amount of N in deficient seedlings w about one-fourth of normal but concentratio were only about one-half of normal (table 7).

Distinguishing symptoms (top), advanc symptoms (bottom) in red maple.

Table 7.—*Average height growth, ovendry seedling weight, nitrogen concentrations and total content component parts of red maple seedlings grown in deficient, complete nutrient, and distilled wat solutions for 117 days*[1]

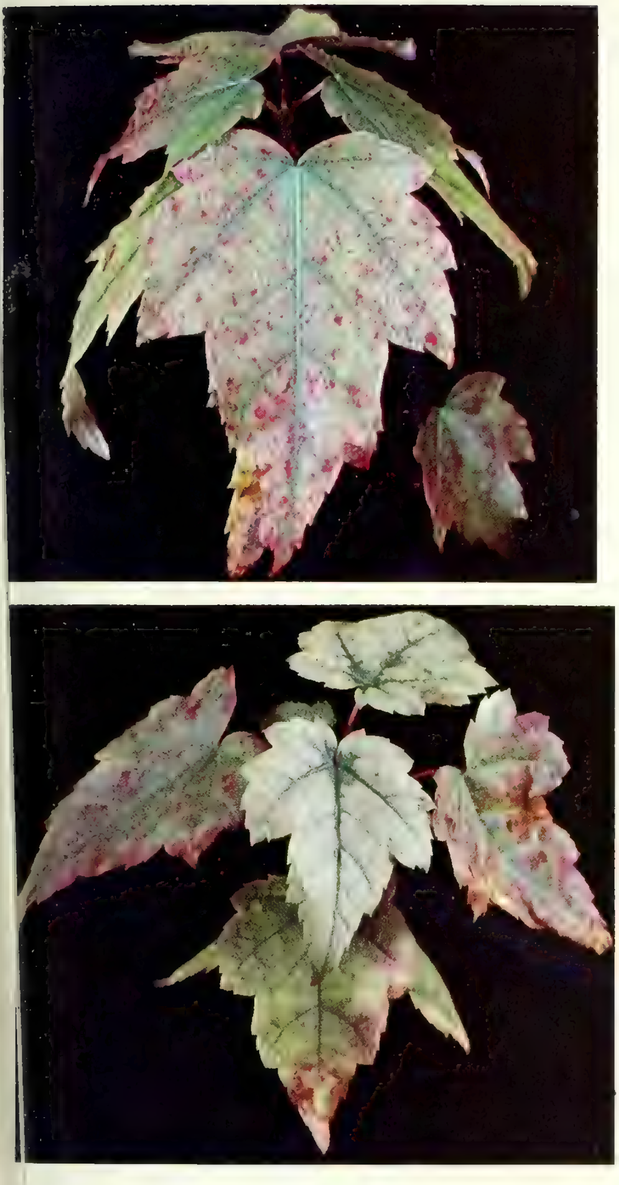
			Nitrogen						
			Concentration			Total Content			
Solution	**Height growth**[2]	**Dry weight**[3]	**Leaves**	**Stem**	**Roots**	**Leaves**	**Stem**	**Roots**	**Plan**
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	154.4	5.83	1.43	0.95	1.31	25.45	10.83	38.12	74.4
Deficient	163.0	2.99	0.71	0.37	0.60	6.74	2.85	7.62	17.21
Water	1.0	0.50	—[4]	—	0.50	—	—	—	—

[1] See Appendix table 29 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.

[4] Dashes indicate that inadequate material was available for chemical analysis.



Phosphorus

Deficiency symptoms

Brown tip scorch and blotching in the lower leaves were the first signals of P deficiency. Then lower leaves turned dull green as upper leaves gradually became mottled dull green, yellow, and red. As the deficiency advanced young leaf tips often scorched while lower leaves developed dull light-green, yellow-green, and red mottles, and marginal scorch. Lower leaves browned completely before they were finally shed.

Growth

Phosphorus-deficient seedlings were stunted, like the distilled water seedlings, and much shorter than any other deficient seedlings. Phosphorus-deficient seedlings had fewer, smaller, and narrower leaves than normal seedlings. Total oven dry weights of P-deficient seedlings were identical to the distilled water controls and about one-tenth that of normal seedlings.

Nutrient content

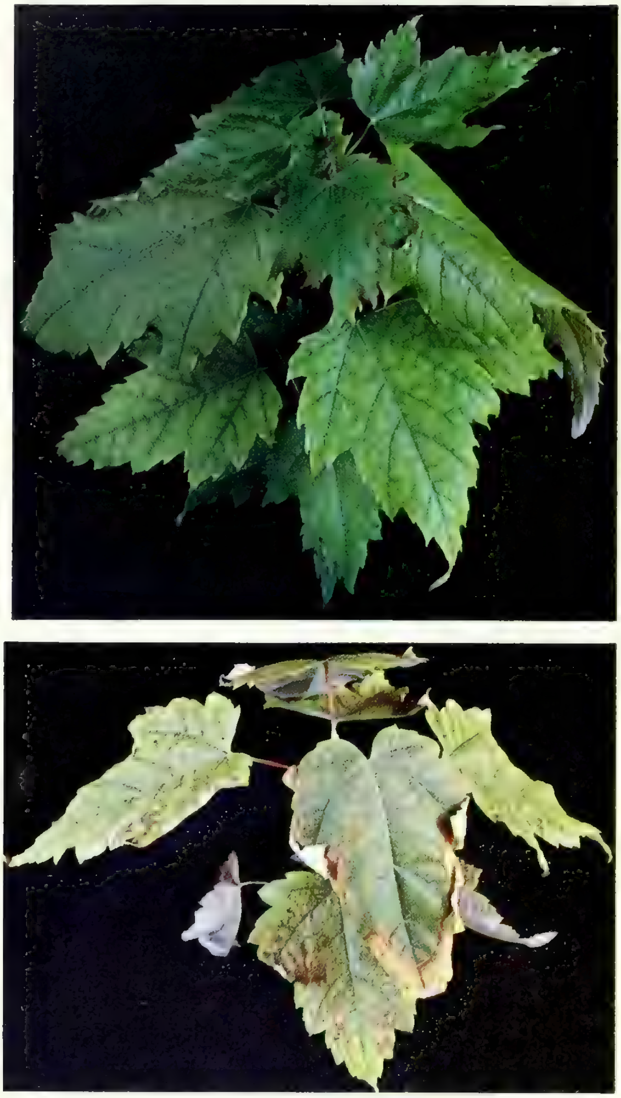
Absolute amount of P in deficient plants was about a fortieth of normal, yet concentrations ranged from about a half to a sixth of normal (table 8).

Distinguishing symptoms (top), advanced symptoms (bottom) in red maple.

Table 8.—*Average height growth, ovendry seedling weight, phosphorus concentrations and total content in component parts of red maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

			Phosphorus						
			Concentration			Total Content			
S ution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
C nplete	154.4	5.83	0.17	0.15	0.25	3.03	1.71	7.28	12.02
D icient	22.6	0.52	0.03	0.07	0.08	0.05	0.06	0.21	0.32
W ter	1.0	0.50	0.04	0.06	0.09	0.04	0.06	0.24	0.34

ee Appendix table 29 for more complete growth data.
eight growth from treatment establishment until harvest.
vendry weight of entire plant.



Distinguishing symptoms (top), advanced symptoms (bottom) in red maple.

Potassium

Deficiency symptoms

Initially, young foliage became lighter yel green, except for the veinal network which mained a contrasting darker green. Young l tips also curled down and then scorched. Margi scorching of young foliage followed, along w salting in both young and old foliage. Salted ar on young foliage coalesced into blotches as lo foliage turned light green and began to roll Finally lower leaves shriveled up, but they w retained on the stem hanging down from horiz tal petioles.

Growth

Potassium-deficient seedlings had shorter, m slender stems with smaller leaves than nor seedlings. Dry weights of K-deficient seedlin were comparable to distilled water seedlin However, K deficiency reduced root and st yields more than foliage yields.

Nutrient content

Total content of K taken up in tissues of defi ent seedlings was reduced by a factor of 8 or mo but concentrations were only 2 to 5 times le (table 9).

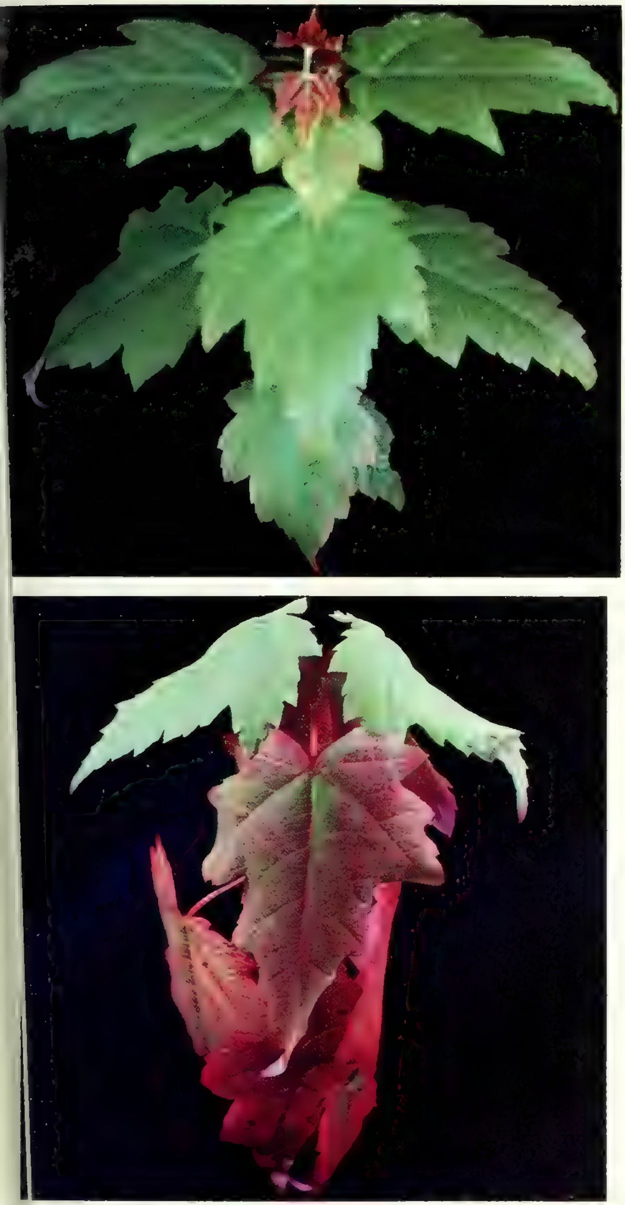
Table 9.—*Average height growth, ovendry seedling weight, potassium concentrations and total content component parts of red maple seedlings grown in deficient, complete nutrient, and distilled wat solutions for 117 days*[1]

			Potassium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	154.4	5.83	0.78	0.36	0.59	13.88	4.10	17.17	35.15
Deficient	60.2	1.45	0.17	0.20	0.28	1.29	0.48	1.26	3.03
Water	1.0	0.50	0.25	0.32	0.42	0.32	0.32	1.13	1.77

[1] See Appendix table 29 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Calcium

Deficiency symptoms

First, young foliage faded from dark green to light green. Then interveinal tissues turned yellowish green while midribs and veins stayed light green. Next symptoms were the curling down of young leaf tips and the appearance of red tips and margins on older foliage. This was followed by necrotic or discolored spotting on leaves of all ages. As the deficiency intensified, foliage from the bottom up the plant changed to first pink, then red, petioles drooped below horizontal, and leaf blades hung vertically.

Growth

Calcium deficiency caused stunting and a great reduction in leaf numbers and their size. Seedling component weight yields were not different than the distilled water controls.

Nutrient content

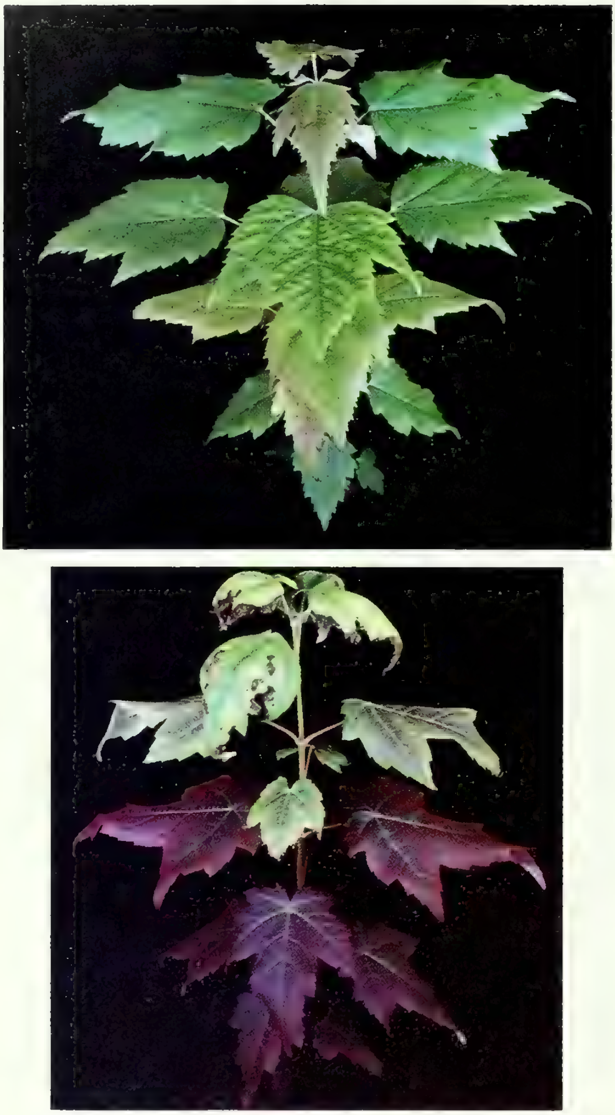
Deficient plants had 21 times less Ca in their tissues than normal plants. The amounts of Ca in root tissues were especially low. Although percentage values showed similar trends, none of the values approached the reductions shown by absolute amounts (table 10).

Distinguishing symptoms (top), advanced symptoms (bottom) in red maple.

T ble 10.—*Average height growth, ovendry seedling weight, calcium concentrations and total content in component parts of red maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

			Calcium						
			Concentration			Total Content			
S ution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	Grams	Percent ovendry weight			Milligrams per seedling			
C nplete	154.4	5.83	2.24	1.12	0.73	39.87	12.77	21.24	73.88
D cient	37.2	1.47	0.53	0.19	0.06	2.60	0.51	0.43	3.54
W er	1.0	0.50	0.85	0.92	0.29	1.10	0.92	0.78	2.80

ee Appendix table 29 for more complete growth data.
eight growth from treatment establishment until harvest.
vendry weight of entire plant.



Distinguishing symptoms (top), advanced symptoms (bottom) in red maple.

Magnesium

Deficiency symptoms

Initially, Mg-deficient seedlings seemed mo luxuriant than seedlings receiving all nutrient The first characteristic symptom appeared as prominent pattern in upper leaves. This patter formed as interveinal tissues faded from the ma gins inward between veins toward the midri leaving a broad, sharp zone of dark-green tissu next to the main veins and midrib. The secon characteristic symptom was the deep-purple col that developed in mature leaves as they becam dominated by anthocyanin pigments. This color tion progressed up the plant, while young leave rolled up and developed tip scorch. After this, ne rotic blotching intensified in older leaves just b fore they were shed from the bottom up the stem

Growth

Magnesium deficiency reduced seedling ro weights below the complete nutrient control lev but foliage and stem weights were not. During th relatively short duration of these studies, the goo height growth of red maple, white ash, and pape birch seedlings in Mg-deficient treatments may b caused by small amounts of Mg remaining in th sand as contaminants, or perhaps by the effect sodium initially partly replacing these specie needs for Mg. These effects under potassium defi ciency are well known (Hewitt 1966).

Nutrient content

Uptake of Mg was reduced considerably. Eithe the percentage values or the total amount of Mg i the foliage appear to be good diagnostic tools fo estimating a seedling's Mg status (table 11).

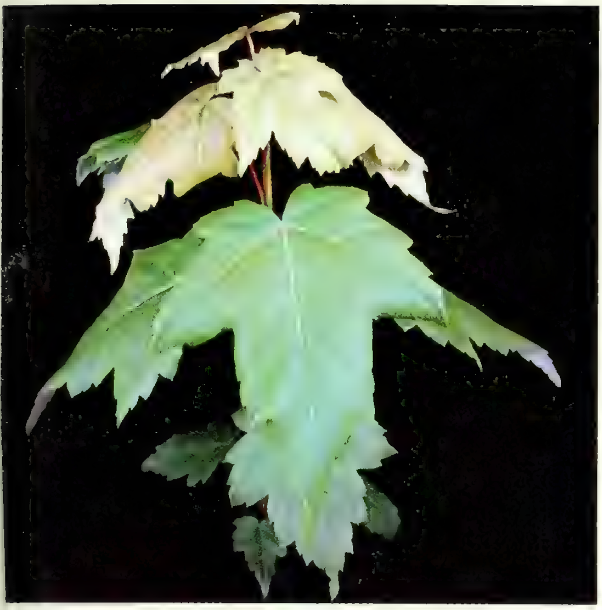
Table 11.—*Average height growth, ovendry seedling weight, magnesium concentrations and total content i component parts of red maple seedlings grown in deficient, complete nutrient, and distilled wate solutions for 117 days*[1]

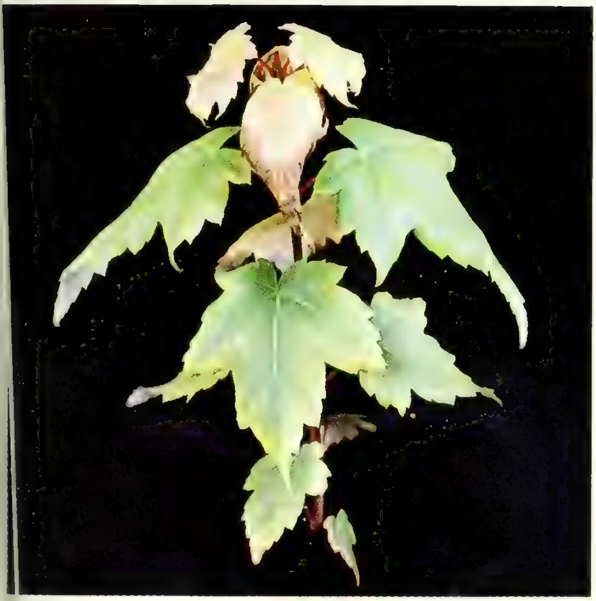
			Magnesium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	154.4	5.83	0.63	0.12	0.19	11.21	1.37	5.53	18.11
Deficient	222.0	4.55	0.04	0.02	0.05	0.85	0.20	0.70	1.75
Water	1.0	0.50	0.24	0.08	0.11	0.31	0.08	0.30	0.69

[1] See Appendix table 29 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.





Sulfur

Deficiency symptoms

First, upper expanding leaf surfaces developed a pink to yellow-green cast and their tips curled under and drooped. Then tip scorch and spotting appeared on these leaves, which was later followed by the spreading of necrotic areas, first along the margins and then inward toward the midrib and petiole. Old lower leaves turned lighter green than normal and finally developed tip scorch.

Growth

Sulfur-deficient seedlings weighed about half as much as the complete nutrient controls after 117 days under treatment. Besides this, the deficiency also noticeably depressed height growth and reduced the size of younger leaves.

Nutrient content

Total amounts of S in deficient seedlings was reduced sixfold, while concentrations indicated about half as much of a reduction from normal levels (table 12).

Distinguishing symptoms (top), advanced symptoms (bottom) in red maple.

Tble 12.—*Average height growth, ovendry seedling weight, sulfur concentrations and total content in component parts of red maple seedlings grown in deficient, complete nutrient, and distilled water solutions for 117 days*[1]

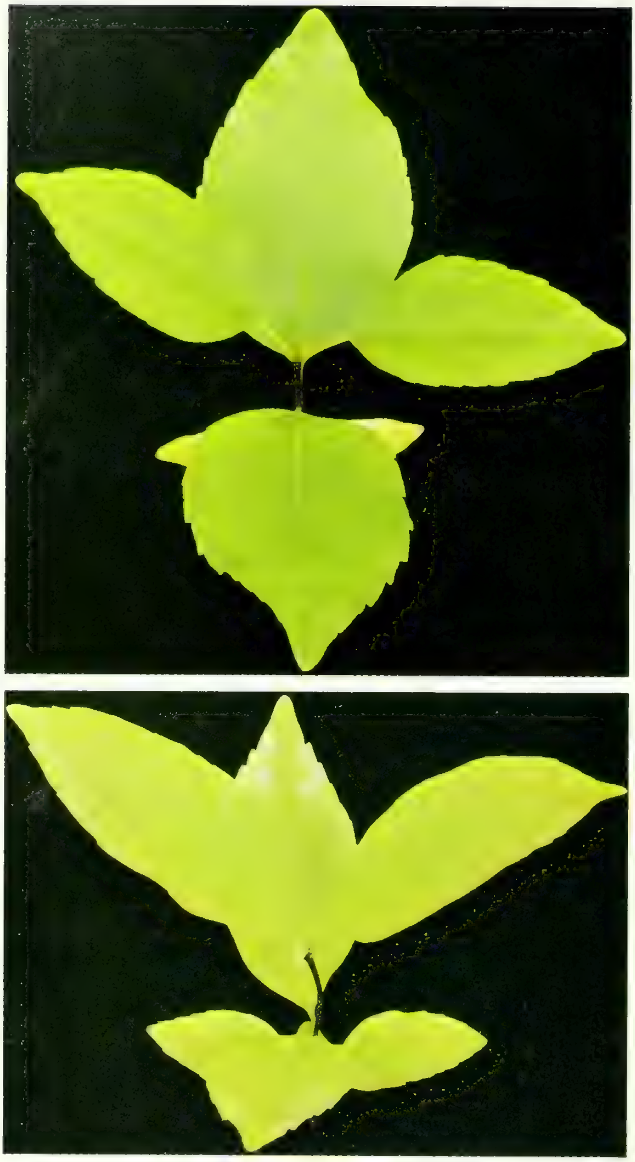
			Sulfur						
			Concentration			Total Content			
Slution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Cnplete	154.4	5.83	0.21	0.08	0.17	3.73	0.91	4.95	9.59
Dcient	79.2	3.02	0.06	0.05	0.05	0.48	0.30	0.81	1.59
Wer	1.0	0.50	—[4]	—	—	—	—	—	—

ee Appendix table 29 for more complete growth data.

eight growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.

[4] Dashes indicate that inadequate material was available for chemical analysis.



Distinguishing symptoms (top), advanced symptoms (bottom) in white ash.

Nitrogen

Deficiency symptoms

Leaves and petioles throughout the white as plants gradually faded to a uniform light-gree color as N became deficient. Following this, th cotelydons and the lowest pair of true leave quickly changed from light green to yellow gree to entirely yellow, while all higher leaves retaine their light-green color. This is the characteristi symptom for N deficiency in most plants. As gree leaves faded, leaf margins and interveinal tissue often developed a purplish cast but no distinctiv patterns were formed. Shortly thereafter, thes symptoms began moving up the stem. Necrosi first appeared on the margins of the yellow cotely dons and subsequently as tip and marginal scorc on the lower leaves. Petioles also became mor erect than normal, having about a 15° angle wit the stem.

Growth

Nitrogen-deficient seedlings generally wer shorter and had smaller leaves than normal seedlings. Deficient seedlings had the lowest total an component weights of the 7 single-element deficiencies studied. Their weights were comparable to distilled water controls and 62 percent below complete nutrient controls.

Nutrient content

Total uptake was about one-sixth of normal and concentrations about half of normal in N-deficient seedlings (table 13).

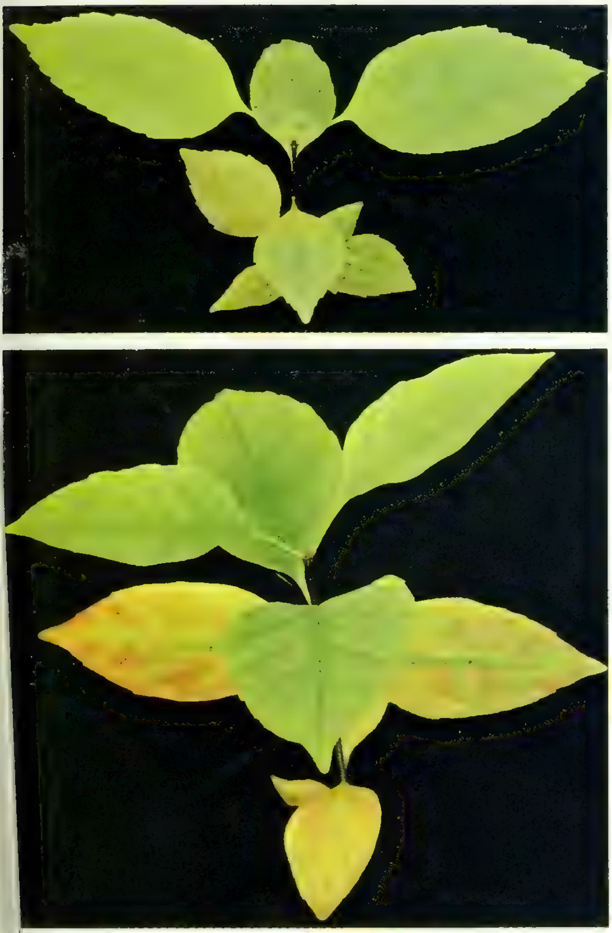
Table 13.— *Average height growth, ovendry seedling weight, nitrogen concentrations and total content in component parts of white ash seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

			Nitrogen						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	62	3.51	1.32	1.10	1.18	9.11	5.61	27.14	41.86
Deficient	28	1.33	0.54	0.77	0.56	1.73	1.54	4.54	7.81
Water	39	1.11	0.40	0.66	0.51	0.96	1.12	3.57	5.65

[1] See Appendix table 30 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Distinguishing symptoms (top), advanced ymptoms (bottom) in white ash.

Phosphorus

Deficiency symptoms

Although foliage might fade slightly at first and some terminal leaves might scorch at the tip, major P-deficiency symptoms began in the lower leaves and slowly progressed up the stem. Shortly after, lower leaves turned lighter green, and purplish spots appeared on them. Next they developed yellow and brown necrotic areas, while upper leaves remained green. Symptoms in the veinal network of lower leaves developed more slowly; the network remained light green as the leaf yellowed and finally turned yellow as the leaf browns.

Growth

Normally, growth reductions would be expected by omitting P, but white ash is a determinate grower and 60 percent of its height growth was already completed before deficiency treatments were begun. Another growing period would be required for the expected reductions to develop.

Nutrient content

Total uptake in tissues of deficient seedlings was one quarter of normal. The reduction in uptake was much greater in foliage than other tissues (table 14).

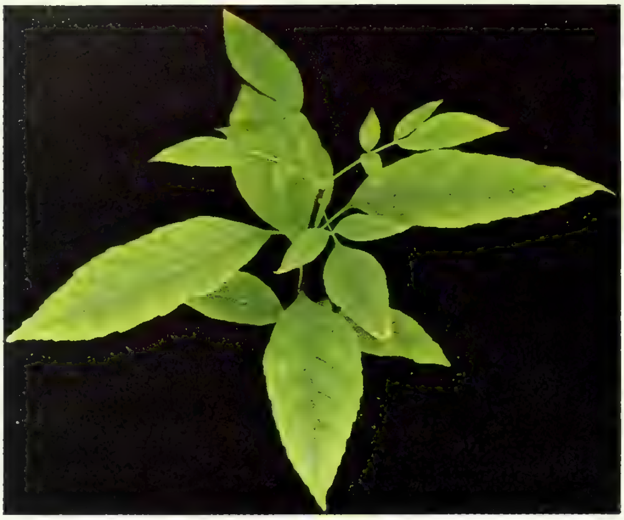
Table 14.—*Average height growth, ovendry seedling weight, phosphorus concentrations and total content in component parts of white ash seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

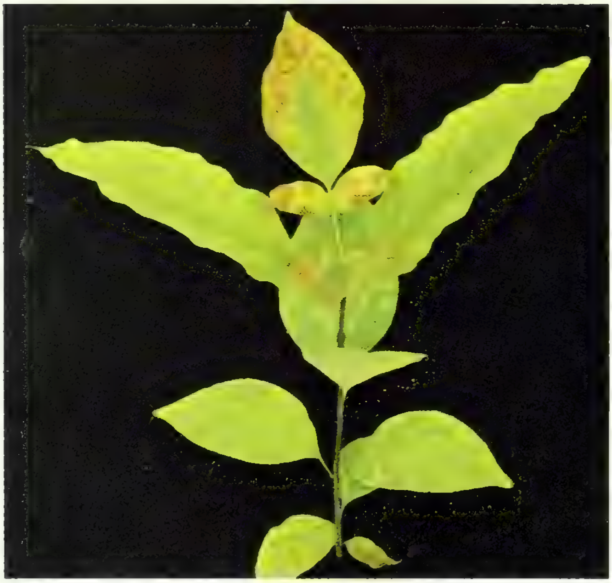
			Phosphorus						
			Concentration			Total Content			
Solution	**Height growth**[2]	**Dry weight**[3]	**Leaves**	**Stem**	**Roots**	**Leaves**	**Stem**	**Roots**	**Plant**
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	62	3.51	0.36	0.14	0.19	2.48	0.71	4.37	7.56
Deficient	68	3.14	0.05	0.06	0.06	0.28	0.30	1.24	1.82
Water	39	1.11	0.10	0.09	0.12	0.24	0.15	0.84	1.23

[1] e Appendix table 30 for more complete growth data.

[2] ight growth from treatment establishment until harvest.

[3] endry weight of entire plant.





Distinguishing symptoms (top), advanced symptoms (bottom) in white ash.

Potassium

Deficiency symptoms

Upper leaves might droop from normally ere petioles before the tips scorched on termina leaves. This was followed by the light-green fadin of upper leaf margins. Finally, all leaf tissue b came the same color, but leaf ribs and bases staye green longer. These symptoms gradually move down the stem to the lowest leaves. In sever stages of K deficiency, upper leaf tips and margin often became completely scorched resulting i curved-up and rolled-in upper leaf margins. Late some tips and edges scorched in lower leaves too

Growth

Height growth was not reduced as expected fc the reasons discussed under growth of P-deficier white ash seedlings.

Nutrient content

Absolute amounts of K in leaf and stem tissue and K-leaf concentrations reflect the reduce uptake of K which averaged about one-third c normal (table 15).

Table 15.—*Average height growth, ovendry seedling weight, potassium concentrations and total content ir component parts of white ash seedlings grown in deficient, complete nutrient, and distilled watei solutions for 113 days*[1]

			Potassium						
			Concentration			**Total Content**			
Solution	**Height growth**[2]	**Dry weight**[3]	**Leaves**	**Stem**	**Roots**	**Leaves**	**Stem**	**Roots**	**Plant**
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	62	3.51	1.42	0.78	0.88	9.80	3.98	20.24	34.02
Deficient	79	3.59	0.27	0.60	0.40	1.89	0.33	9.40	11.62
Water	39	1.11	0.62	0.60	0.60	1.49	1.02	4.20	6.71

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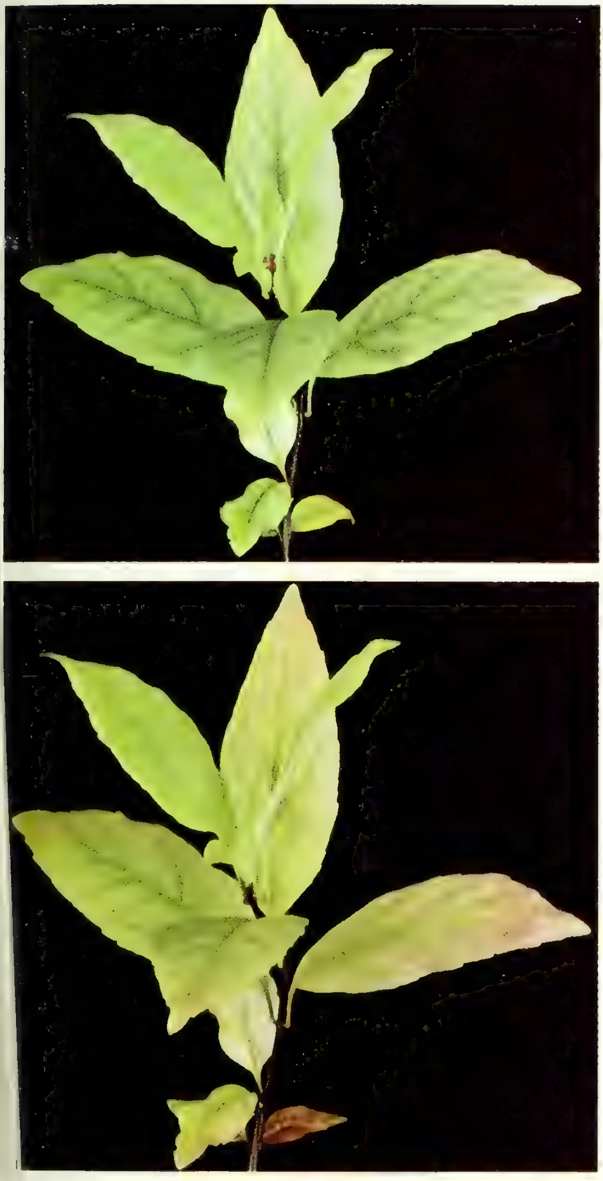
[1] See Appendix table 30 for more complete growth data.
[2] Height growth from treatment establishment until harvest.
[3] Ovendry weight of entire plant.



Distinguishing symptoms (top), advanced symptoms (bottom) in white ash.

Calcium

Deficiency symptoms

Early symptoms of Ca deficiency were tip scorching of terminal leaves, death of uncurling new leaves and growing tips, and erect petioles that almost parallel the stem. In extreme cases petioles of terminal leaf pairs crossed each other. Fading at first resulted in uniform light-green leaves and petioles, but then intensified in interveinal areas to a very pale green to whitish green to a whitish yellow, with some areas almost white. Through the early interveinal color changes tissues around leaf midribs and major veins remained light green. In severe stages, water-soaked-looking blotches appeared on the edges, and the interveinal tissues scorched. Similar symptoms appeared later on lower leaves.

Growth

Stems and leaves appeared smaller than normal on Ca-deficient plants. Root weights of deficient plants were especially low, being 60 percent below normal levels and comparable to distilled water controls.

Nutrient content

Total Ca uptake was a sixth and concentrations about a fourth of normal levels (table 16).

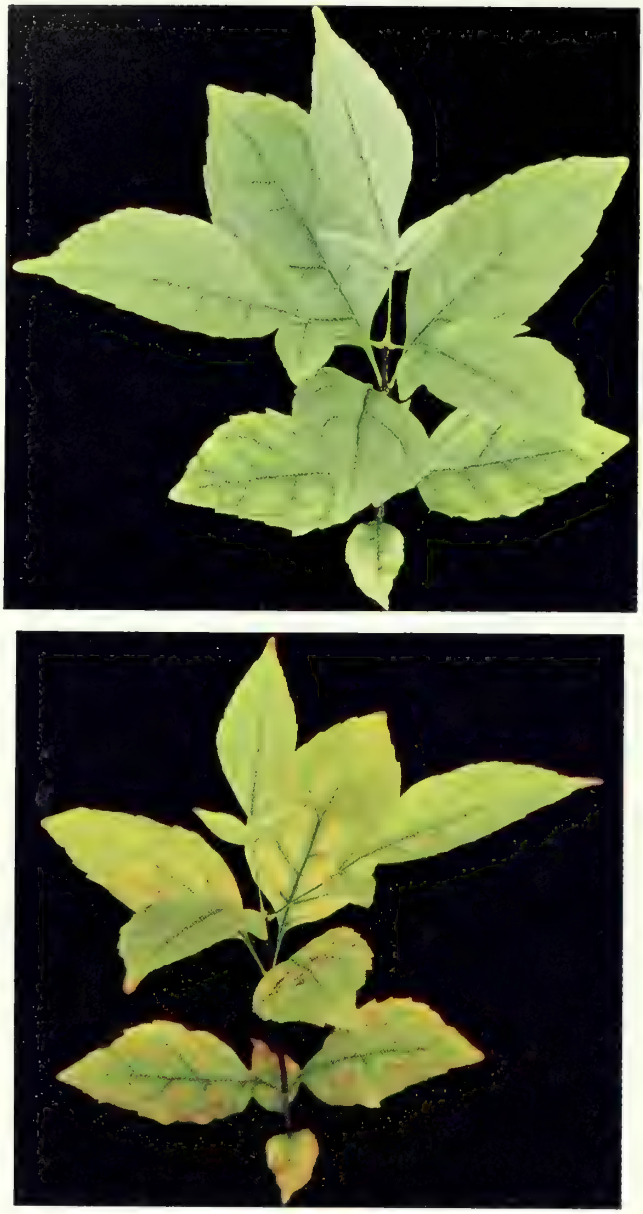
able 16.— *Average height growth, ovendry seedling weight, calcium concentrations and total content in component parts of white ash seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

			Calcium						
			Concentration			Total Content			
S ution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
C nplete	62	3.51	1.31	0.64	0.40	9.04	3.26	9.20	21.50
D icient	56	1.79	0.39	0.15	0.09	1.91	0.58	0.82	3.31
W er	39	1.11	0.78	0.55	0.25	1.87	0.94	1.75	4.56

ee Appendix table 30 for more complete growth data.

eight growth from treatment establishment until harvest.

vendry weight of entire plant.



Magnesium

Deficiency symptoms

Distinctive symptoms of Mg deficiency first a
peared in the lower two pairs of leaves, but soo
were present even in the youngest foliage. Le
tips, margins, and interveinal areas first faded to
light green, then to a yellow-green, and finall
yellow dominated. Tissues next to the veinal ne
work, midribs, and point of petiole attachmen
remained green, contrasting with other yello
leaf tissues. A purplish discoloration often pr
ceded necrosis that began at leaf tips and late
appeared at leaf margins and between veins.

Growth

Root weights of Mg-deficient seedlings wer
slightly lower (14 percent) than those of complet
nutrient controls. Usually, the aboveground po
tions of Mg-deficient seedlings looked healthy unt
the deficiency was well developed. (See discussio
of growth of Mg-deficient red maple seedlings.)

Nutrient content

Total Mg uptake and concentrations were abou
one-fourth that of normal seedlings (table 17).

Distinguishing symptoms (top), advance
symptoms (bottom) in white ash.

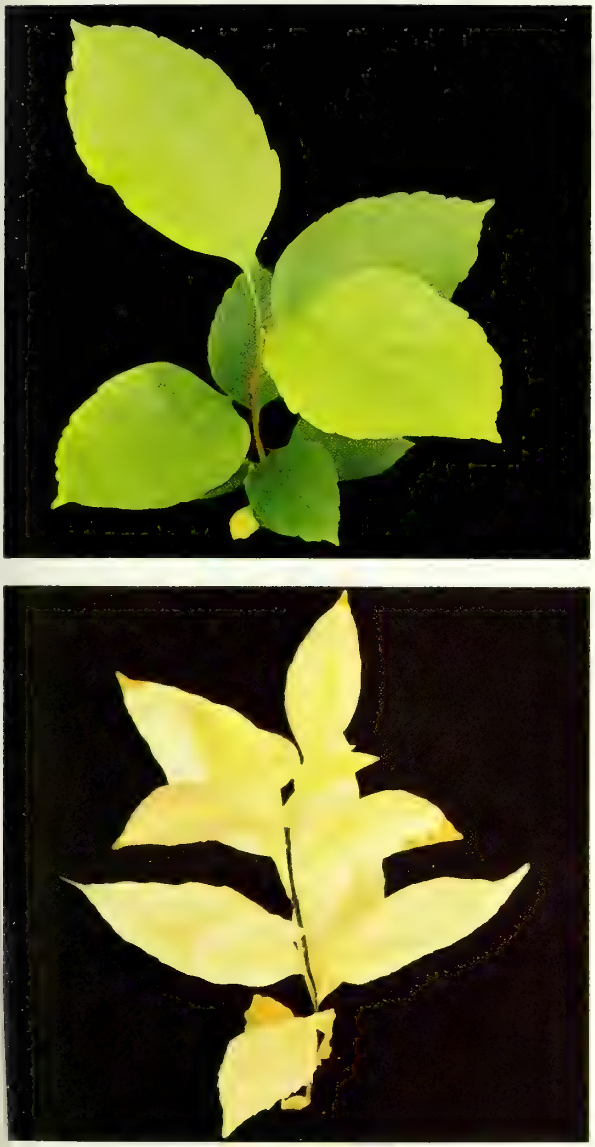
Table 17.—*Average height growth, ovendry seedling weight, magnesium concentrations and total content i*
component parts of white ash seedlings grown in deficient, complete nutrient, and distilled wate
solutions for 113 days[1]

			Magnesium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	62	3.51	0.25	0.14	0.13	1.72	0.71	2.99	5.42
Deficient	117	3.41	0.04	0.05	0.04	0.33	0.31	0.79	1.43
Water	39	1.11	0.13	0.11	0.10	0.31	0.19	0.70	1.20

[1] See Appendix table 30 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Sulfur

Deficiency symptoms

Characteristic symptoms of S deficiency in white ash first appeared when young upper leaves turned lighter green than lower leaves. Newly emerging upper leaves often rolled under and wrinkled. Then, leaves throughout the plant became a uniform yellow-green color. Tip scorch and spotting also occurred simultaneously on the upper and middle leaves of some plants. In more advanced stages new growing points often died, and upper leaves turned entirely yellow except for tips and other scorched spots.

Growth

Root weight was reduced (36 percent) by the omission of S. Other expected growth reductions did not occur as already explained under the growth section for P-deficient seedlings.

Nutrient content

Total uptake of S in deficient seedling was about a third of normal (table 18).

Distinguishing symptoms (top), advanced symptoms (bottom) in white ash.

able 18.— *Average height growth, ovendry seedling weight, sulfur concentrations and total content in component parts of white ash seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

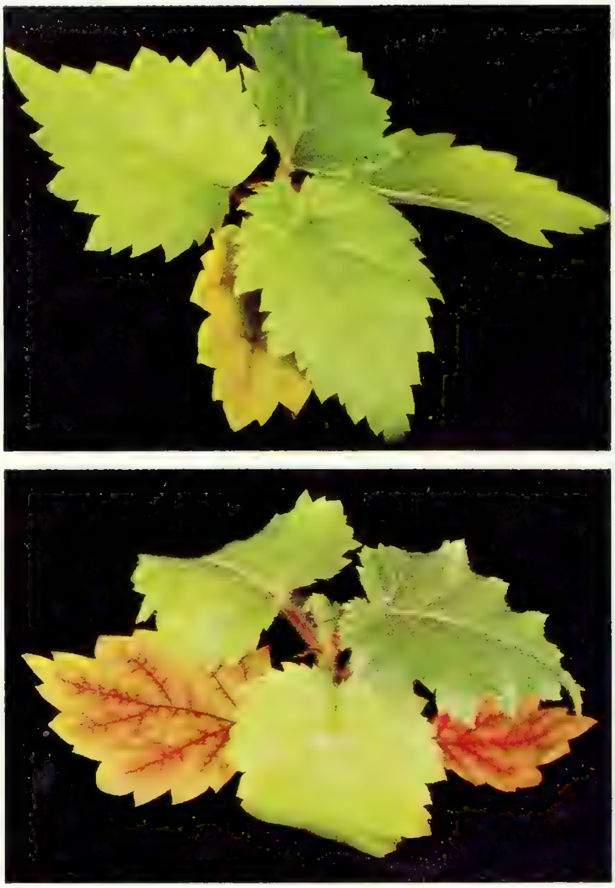
			Sulfur						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Cmplete	62	3.51	0.15	0.07	0.09	1.04	0.36	2.07	3.47
Dficient	83	2.62	0.06	0.05	0.04	0.38	0.25	0.59	1.22
Wter	39	1.11	-[4]	-	-	-	-	-	-

ee Appendix table 30 for more complete growth data.

eight growth from treatment establishment until harvest.

vendry weight of entire plant.

ashes indicate that inadequate material was available for chemical analysis.



Distinguishing symptoms (top), advanced symptoms (bottom) in paper birch.

PAPER BIRCH

Nitrogen

Deficiency symptoms

Foliage throughout N-deficient paper birch seedlings quickly faded to a uniform light-green color while midribs and veins on the lowest leaves turned red. Shortly thereafter, oldest (lower leaves turned yellow but their midribs and veins remained red. These symptoms gradually progressed up the stem while the lower leaves often tip scorched before they turned completely brown and abscised.

Growth

Omission of N caused the greatest growth suppression of the six elements studied. Stunted N-deficient plants looked like those plants grown in distilled water. Leaf production was drastically curtailed in N-deficient plants and leaves were smaller in size. Dry weight yields of leaves, stems, and roots were reduced to only about 10 percent of the complete nutrient controls. (See Appendix table 31 for more information.)

Nutrient content

Uptake was drastically curtailed in N-deficient plants. Absolute amounts of N averaged one-sixteenth of normal, but concentrations ranged from nearly equal in stems and roots to about half normal levels in the foliage (table 19).

Table 19.— *Average height growth, ovendry seedling weight, nitrogen concentrations and total content in component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

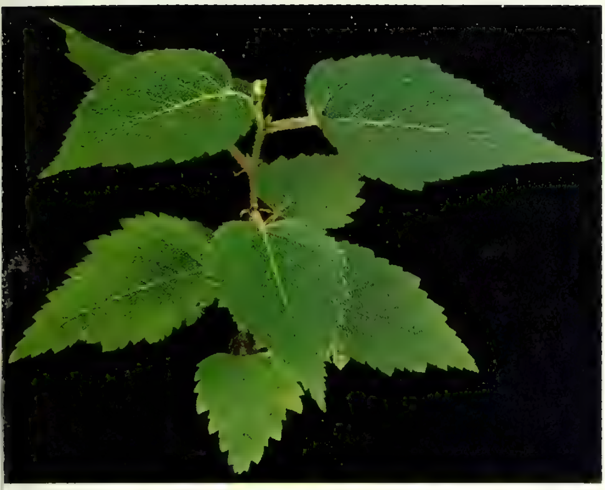
			Nitrogen						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	179	4.59	1.12	0.62	0.95	18.48	4.09	21.66	44.23
Deficient	17	0.40	0.52	0.60	0.85	0.88	0.30	1.53	2.71
Water	10	0.35	0.44	-[4]	0.66	0.62	-	1.06	-

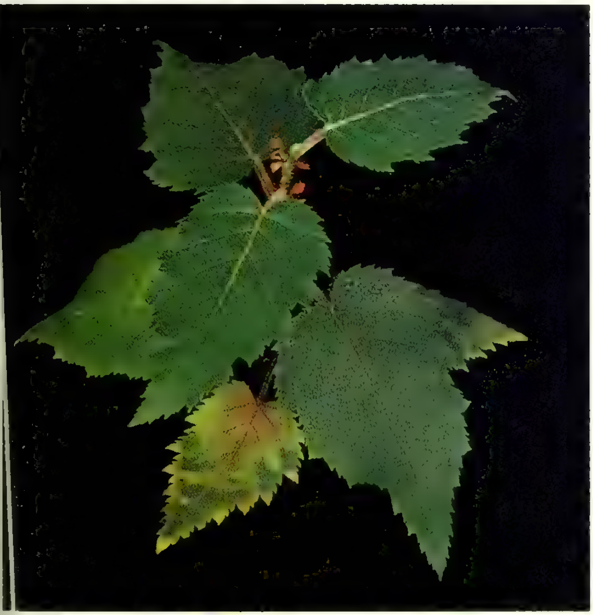
[1] See Appendix table 31 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.

[4] Dashes indicate that inadequate material was available for chemical analysis.





Distinguishing symptoms (top), advanced symptoms (bottom) in paper birch.

Phosphorus

Deficiency symptoms

Visual foliar symptoms of P deficiency were slow in showing up. At first, all leaves turned darker green and duller than normal. After this, dull light-green and later dull yellow-green areas appeared at the tips, serrated edges, and in irregular patches on the lower leaves. Then, chlorotic leaf tips, edges, and some blotches turned brown as the symptoms spread across the leaf and began to move up the stem. In later stages, brown leaf tips curled up before the leaves became entirely brown and abscised.

Growth

Height growth was also restricted by the omission of P, but not to the same extent as in N-deficient seedlings. Upper leaves on P-deficient seedlings were noticeably narrower in width than normal leaves but not in length. Average dry weight yields of birch foliage, stems, and roots were reduced 62, 47, and 60 percent by P deficiency, respectively.

Nutrient content

Total P uptake— especially in the foliage— was greatly reduced by its omission from the cultural solution. Concentrations showed similar patterns but their magnitude was not as great (table 20).

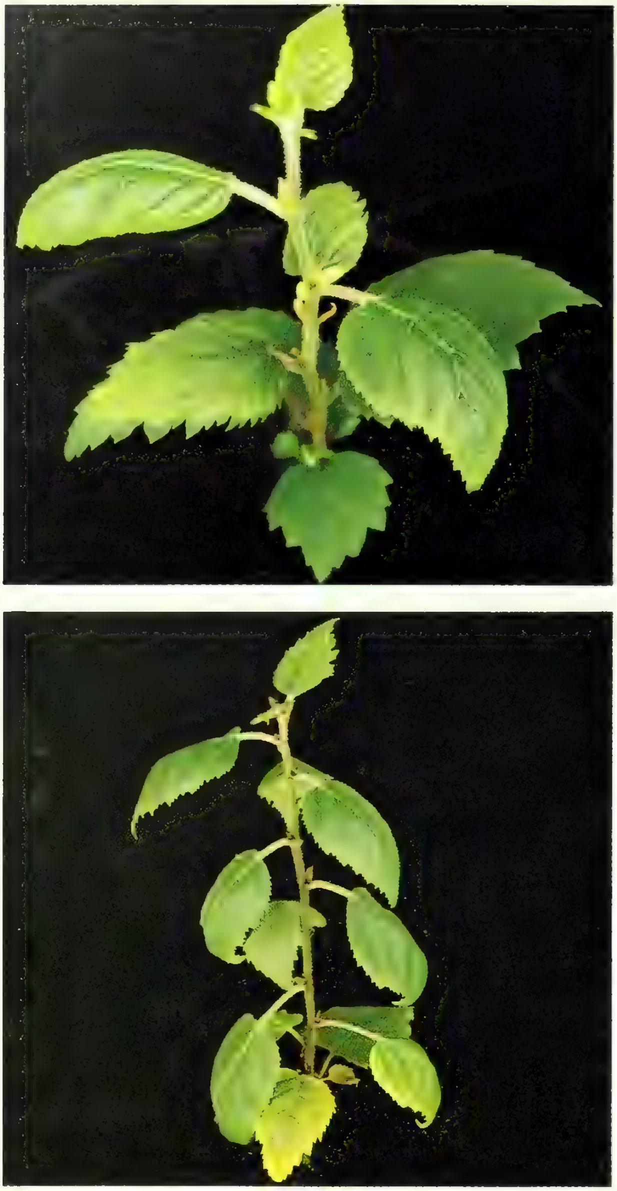
Table 20.—*Average height growth, ovendry seedling weight, phosphorus concentrations and total content in component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

			Phosphorus						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	179	4.59	0.51	0.19	0.21	8.42	1.25	4.79	14.46
Deficient	100	1.88	0.03	0.04	0.09	0.19	0.14	0.82	1.15
Water	10	0.35	0.28	0.14	0.19	0.39	0.07	0.30	0.76

[1] See Appendix table 31 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Potassium

Deficiency symptoms

First symptoms of K deficiency appeared in th upper leaves before any color change in the lowe leaves took place. The upper leaves on some plant buckled under along the midribs and curved unde at the margins. Then lower leaf tips, serration margins, and finally interveinal tissues, from th margins toward the midribs, gradually began t turn from light green to yellow green to yellow This was followed by leaf tip and edge scorch in th lower leaves.

Growth

After growing in K-deficient solutions for 11 days, birch seedlings exhibited only slight differ ences in growth from normal seedlings.

Nutrient content

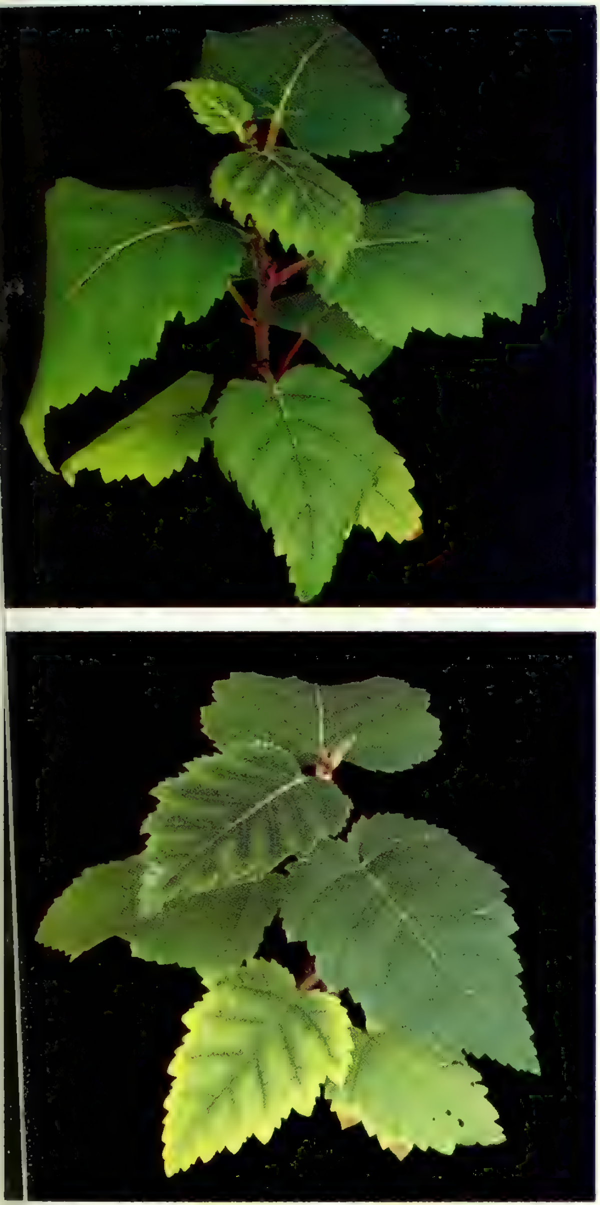
Total content of K was about a third of normal i deficient plants. Percentage values in tissue showed similar decreases (table 21).

Distinguishing symptoms (top), advance symptoms (bottom) in paper birch.

Table 21.—*Average height growth, ovendry seedling weight, potassium concentrations and total content i component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled wate solutions for 113 days*[1]

			Potassium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	179	4.59	1.46	0.40	0.52	24.09	2.64	11.86	38.59
Deficient	171	4.78	0.39	0.16	0.20	6.28	1.20	4.86	12.34
Water	10	0.35	1.14	0.36	0.33	1.60	0.18	0.53	2.31

[1] See Appendix table 31 for more complete growth data.
[2] Height growth from treatment establishment until harvest.
[3] Ovendry weight of entire plant.



Calcium

Deficiency symptoms

All foliage slowly faded to a uniform light green with basal leaves often appearing even paler. Interveinal areas on the lower one or two leaves finally turned pale yellow; narrow bands of light green remained next to the veins and midribs. After yellowing, the tips and serrated edges of lower leaves scorched; water-soaked blotches sometimes appeared on them. Another advanced symptom was the "hooking down" of young leaf tips.

Occasionally veins in basal leaves appeared much like those on N-deficient seedlings. However, in Ca-deficient seedlings the colored vein symptom occurred much later, was not as sharply defined, and appeared more as a reddish or pinkish cast around the veinal network.

Growth

Calcium deficient seedlings had fewer leaves and were about half as tall as normal seedlings. Deficient seedling weights averaged 47 percent below controls; 52 percent reductions occurred in both stems and roots and a 39 percent reduction in the foliage.

Nutrient content

Absolute uptake of Ca in tissues was a tenth to a twentieth of normal, but concentrations were only a fifth to a tenth of normal (table 22).

Distinguishing symptoms (top), advanced symptoms (bottom) in paper birch.

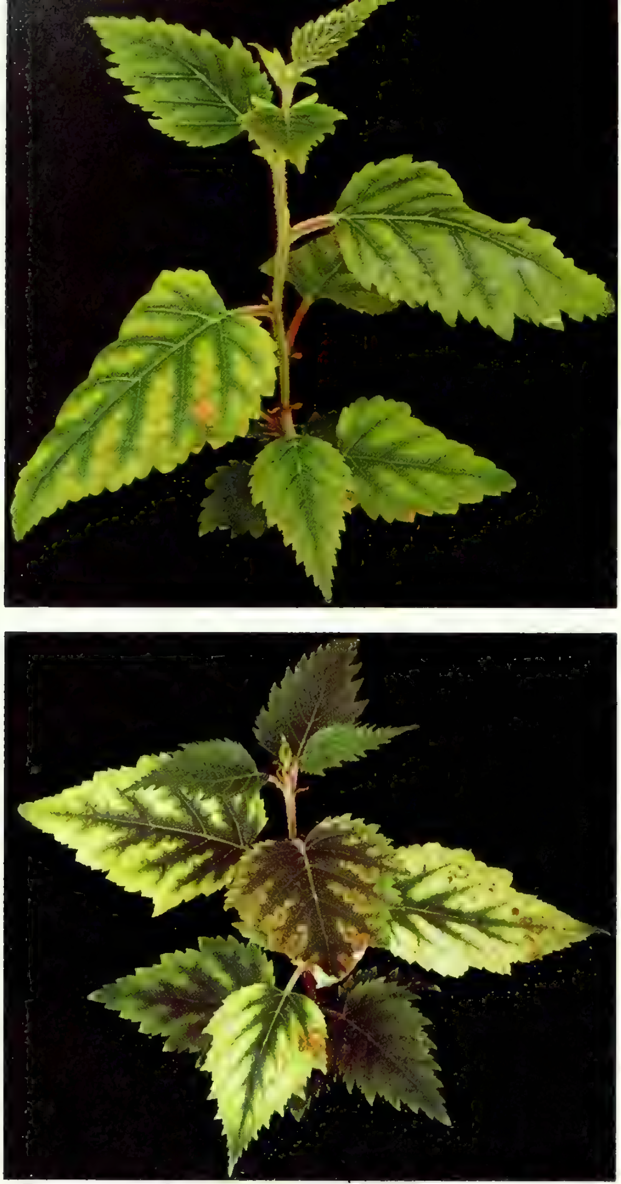
Table 22.— *Average height growth, ovendry seedling weight, calcium concentrations and total content in component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

			Calcium						
			Concentration			Total Content			
Solution	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	179	4.59	1.87	1.10	0.68	30.86	7.26	15.50	53.62
Deficient	69	2.43	0.33	0.11	0.14	3.33	0.35	1.54	5.22
Water	10	0.35	1.19	1.17	0.53	1.67	0.58	0.85	3.10

[1] See Appendix table 31 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Distinguishing symptoms (top), advanced symptoms (bottom) in paper birch.

Magnesium

Deficiency symptoms

A very distinctive chlorotic pattern develope on all but the youngest leaves in Mg-deficient p per birch. Tips, margins, and tissues betwee veins on mature lower and middle leaves fir became light green, while broad bands of tissu adjacent to midribs and main veins, at the bas and sometimes at the tip remained dark gree Light-green margins and interveinal tissues gra ually changed to yellow green, then almost whit Some mature leaf tips scorched early, then, afte tissues had lightened considerably, necrotic spo ting and blotching advanced rapidly.

Growth

Omission of Mg inhibited birch root and foliag growth more than stem growth. Root weights, a ter 113 days under treatment, were only half normal, while total weights were about 34 perce below normal levels. (See discussion of growth Mg-deficient red maple seedlings.)

Nutrient content

The greatest reduction of Mg uptake from no mal occurred in the leaves; the entire plant took u one-twelfth of normal amounts. Deficient tissu concentrations ran from one-fourth to one-fou teenth of normal (table 23).

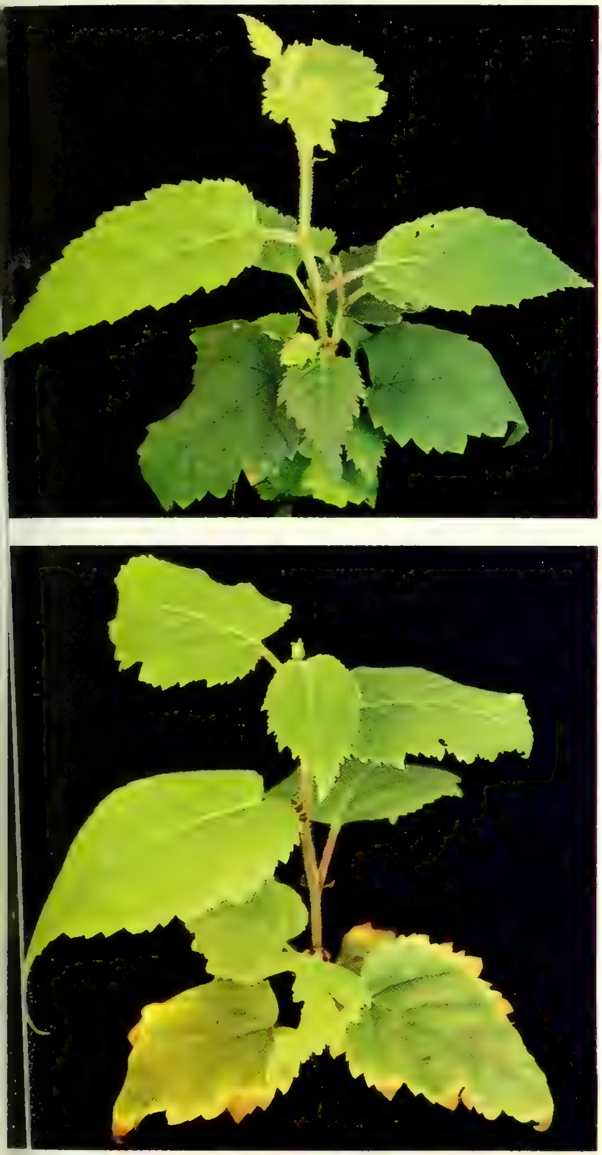
Table 23.—*Average height growth, ovendry seedling weight, magnesium concentrations and total content i component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled wate solutions for 113 days*[1]

Solution	Height growth[2]	Dry weight[3]	Magnesium: Concentration: Leaves	Stem	Roots	Total Content: Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Complete	179	4.59	0.58	0.12	0.14	9.57	0.79	3.19	13.55
Deficient	191	3.02	0.04	0.02	0.04	0.55	0.09	0.47	1.11
Water	10	0.35	0.35	0.14	0.13	0.49	0.07	0.21	0.77

[1] See Appendix table 31 for more complete growth data.

[2] Height growth from treatment establishment until harvest.

[3] Ovendry weight of entire plant.



Sulfur

Deficiency symptoms

Curling down and scorching of newly emerging upper leaf tips and edge serrations often were the first visible signs of S deficiency. New paper birch leaves, developing after deficiencies began, were much more yellow-green than the older foliage which remained dark green, except for yellowing of leaf tips and serrations. Later, old foliage faded to the same color as the new foliage, but leaf tips and margins were either yellow or scorched. Finally, necrotic spotting and edge blotching appeared in the oldest foliage.

Growth

Sulfur-deficient seedlings were slightly smaller than normal and the development of new foliage appeared especially limited. Sulfur deficiency, like Mg deficiency, restricted root and foliage development more than stem development. Total seedling dry weights were reduced 37 percent below normal levels by this deficiency.

Nutrient content

S uptake was reduced primarily in the foliage (table 24).

Distinguishing symptoms (top), advanced symptoms (bottom) in paper birch.

T ble 24.— *Average height growth, ovendry seedling weight, sulfur concentrations and total content in component parts of paper birch seedlings grown in deficient, complete nutrient, and distilled water solutions for 113 days*[1]

			Sulfur						
			Concentration			Total Content			
So tion	Height growth[2]	Dry weight[3]	Leaves	Stem	Roots	Leaves	Stem	Roots	Plant
	Mm	*Grams*	*Percent ovendry weight*			*Milligrams per seedling*			
Co plete	179	4.59	0.22	0.06	0.04	3.63	0.40	0.91	4.94
De ient	128	2.88	0.05	0.04	0.05	0.58	0.22	0.59	1.41
Wa r	10	0.35	-[4]	-	-	-	-	-	-

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[1] S Appendix table 31 for more complete growth data.

[2] ght growth from treatment establishment until harvest.

[3] C ndry weight of entire plant.

[4] D hes indicate that inadequate material was available for chemical analysis.

DISCUSSION

Visual foliar symptoms of nutrient deficiencies should not be used alone for diagnosis because deficiencies of one element may be difficult to distinguish from another element and they can resemble damage caused by insects, disease, climate, and pollution. Smith (1976) reported that leaf symptoms of green veins with yellow interveinal tissue in red maple, are similar for manganese and iron deficiency and are often confused. According to Worswick (1950), micronutrient deficiencies of manganese and copper are difficult to distinguish from K-deficiency in fruit trees. Marginal leaf and tip browning caused by high temperature, leaf scorch following hot drying winds, and fluoride injury may all resemble K deficiency (U.S. Department of Agriculture, Forest Service 1973).

Visual deficiency symptoms usually will not be as well defined in nature as in our experiments because they may be the result of interactions or may be confounded by other deficiency or toxicity symptoms. Thus, visual foliar symptoms can be the first clue to which element might be limiting growth, but chemical analysis should be used to confirm the suspected deficiency.

Samples from the foliage are normally analyzed, but sometimes other parts provide a better critical diagnosis (Hewitt 1966). Often a chemical soil analysis of available nutrients is made, in addition to the other diagnostic measurements, to give a more complete picture of the nutrient status of the trees in nurseries and in field fertilization programs. Foliar analysis for trees is reviewed by Leaf (1973) and van den Driessche (1974). These procedures are not yet routine and the results of chemical analysis of soils or plant tissue must be interpreted and applied carefully.

In our study, all leaves, regardless of maturity, were harvested to make chemical analyses. The seedlings we analyzed generally showed moderate to severe deficiency symptoms. Any seedlings at these deficiency levels would be under severe nutrient stress so foliar symptoms would be very apparent. When symptoms are not so clear or when growth is being restricted making a differential diagnosis requires careful sampling, chemical analysis of the foliage, and expert advice (Phares and Finn 1972). Common sense is required in making a correct diagnosis too, to assure that frost, drought, and diseases (Phares and Finn 1972) or air pollution (U.S. Department of Agricultu Forest Service 1973) are not causing the suspect nutrient problem.

Users wishing to make comparisons with o data for determining whether a nutrient deficie cy exists, should collect all the leaves from a ra dom sample of 10 seedlings in a suspected bed unit after 115 days or in mid-August. Make su the leaves are clean and avoid collecting the within several days after rain because of nutrie leaching (Phares and Finn 1972). The sample including leaves and petioles, should be collect in paper bags and air dried.

Compare the laboratory test results with o "complete" and "deficient" levels. Any levels at above our "complete" nutrient control levels (e cept possibly N which should be somewhat high and is discussed below) are probably within range of concentrations satisfactory for growt Levels approaching our "deficient" levels wou limit growth.

Results of these chemical analyses are applicab to seedlings grown under greenhouse, laborator and nursery conditions, but *not* to forest-grow seedlings or those under field conditions where onl mature leaves are normally collected and analyze and where leaf maturity, leaf position, and seaso al variation in mineral absorption are taken int account in sampling the nutrient content of foliage

Critical deficiency, toxicity, and adequate nutrient supply levels have not been established fo most of the northern hardwood species. However Bjorkbom (1973) reported tentative optimum levels of 3 to 4 percent of foliar N as being adequate fo birch seedlings. His results indicate that our N level was below that required for optimum seedling growth. Other leads from field studies, although not directly comparable, suggest that th foliar levels of N in our complete nutrient control were not optimum for seedling growth. From fiel studies, Mitchell and Chandler (1939) estimate "optimum" foliar N levels for mature sugar maple trees to range from 2.77 to 2.85 percent. Our complete nutrient control foliar N level of 2.24 percent is within their adequate "working region" of 1.7 to 2.77 percent N. Their region where N was limiting growth was below 1.75 percent. Mader *et al.* (1969) considered foliar N levels below 1.50 percent important in sugar maple decline. Mitchell and Chandler (1939) also estimated optimum and other critical leaf N concentrations for red maple and white ash trees. Our foliar N levels of 1.43 percent N for red maple and 1.32 percent N for white ash seedlings (complete nutrient solution) are beginning to limit growth.

In western Massachusetts, Mader *et al.* (1969) associated sugar maple decline with N deficiency, described foliar symptoms typical of N deficiency, and showed a positive response to N fertilization in affected trees.

Bjorkbom (1973) found that paper birch seedlings were not greatly affected by different levels of phosphorus or potassium. In New York, Walker (1956) described foliar symptoms of K deficiency occurring in red maple growing on abandoned farms in K-deficient glacial outwash sands. Walker (1956) considered about 0.60 percent foliar K in mid-August as the point where deficiency symptoms would be expected to appear under field conditions.

Besides the clues from field studies, tables of natural foliar nutrient concentrations have been published that may also be used as guides in forests (Gerloff, Moore, and Curtis 1964, Henry 1973).

Practical methods for correcting nutrient deficiencies are available from agriculture and various forest studies (Beaton 1973) but very few from fertilization trials of northern hardwoods. In general, success in correcting deficiencies has been achieved with both soil applications and foliar sprays of the appropriate fertilizers. This is a rapidly expanding field and the reader is encouraged o consult the various testing agencies (Auhmoody and Filip 1973) for advice. Foliar and soil hemical analyses can be purchased from state xtension services and universities.

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APPENDIX

Table 25.— *Composition of the complete nutrient solution*

Compound or salt	Molarity
MACRONUTRIENTS	
KNO_3	0.002
$Ca(NO_3)_2 \cdot 4H_2O$	0.003
$MgSO_4 \cdot 7H_2O$	0.002
KH_2PO_4	0.002
MICRONUTRIENTS	
FE-EDTA	0.0000891
H_3BO_3	0.0000374
$MnCl_2 \cdot 4H_2O$	0.0000070
$ZnCl_2$	0.0000007
$CuCl_2 \cdot 2H_2O$	0.0000003
MoO_3	0.0000003

able 26.—*Composition of the substitute salt solutions for deficient cultures showing solutions to omit and to replace*

Deficiency	Omit	Replace with
–N	KNO_3, $Ca(NO_3)_2 \cdot 4H_2O$	0.002M KCl, 0.003M $CaCl_2 \cdot 6H_2O$
–P	KH_2PO_4	0.002M KCl
–K	KNO_3, KH_2PO_4	0.002M NaH_2PO_4, 0.002M $NaNO_3$
–Ca	$Ca(NO_3)_2 \cdot 4H_2O$, $MgSO_4 \cdot 7H_2O$	0.002M Na_2SO_4, 0.003M $Mg(NO_3)_2 \cdot 6H_2O$
–Mg	$MgSO_4 \cdot 7H_2O$	0.002M Na_2SO_4
–S	$MgSO_4 \cdot 7H_2O$	0.002M $MgCl_2 \cdot 6H_2O$

Table 27.—*Average nutrient concentrations in foliage, stems, and roots of complete nutrient control seedlings*

						FOLIAGE					
Species	**N**	**P**	**K**	**Ca**	**Mg**	**S**	**Fe**	**Zn**	**Cu**	**Mn**	**B**
	Percent ovendry weight								*p.p.m.*		
Sugar maple	2.24	0.16	0.90	2.38	0.43	0.19	129	14.5	2.6	19.3	43.7
Red maple	1.43	.17	.78	2.24	.63	.21	127	12.5	2.2	14.8	44.9
White ash	1.32	.36	1.42	1.31	.25	.15	194	16.2	3.0	43.2	24.7
Paper birch	1.12	.51	1.46	1.87	1.17	.22	252	9.6	2.0	48.0	65.3
						STEMS					
Sugar maple	1.88	.24	.57	1.43	.16	.15	32	11.5	2.8	29.8	21.9
Red maple	.95	.15	.36	1.12	.12	.08	40	8.0	2.7	6.7	10.1
White ash	1.10	.14	.78	.64	.14	.07	30	5.5	.7	19.3	19.2
Paper birch	.62	.19	.40	1.10	.12	.06	52	12.8	3.2	10.4	12.2
						ROOTS					
Sugar maple	1.83	.24	.94	.76	.30	.26	211	33.0	7.2	8.5	8.8
Red maple	1.31	.25	.59	.73	.19	.17	200	22.4	10.2	6.4	5.3
White ash	1.18	.19	.88	.40	.13	.09	50	14.6	4.0	7.1	13.4
Paper birch	.95	.21	.52	.68	.14	.04	448	209.4	99.9	12.0	9.4

Table 28.—*Average height growth, stem height, number of leaves, ovendry weight of foliage, stem, and root of sugar maple seedlings after 117 days under deficiency treatments*

				Average dry weight per seedling			
Treatment	**Height growth**[1]	**Height**[3]	**Number of leaves**	**Foliage**	**Stem**	**Root**	**Total**
	mm			*gms*			
Complete	27.4 ab[2]	100 a	12.0 a	1.46 a	0.44 a	2.42 a	4.32 a
D–H_2O	2.2 c	78 a	7.2 bc	0.43 c	0.11 d	0.50 e	1.04 d
–N	3.0 c	74 a	6.0 c	0.39 c	0.18 cd	1.16 bcd	1.73 cd
–P	3.2 c	74 a	6.6 bc	0.44 c	0.18 cd	0.84 cde	1.46 cd
–K	10.6 abc	80 a	9.0 abc	0.85 b	0.18 cd	0.62 de	1.65 cd
–Ca	4.6 c	81 a	6.8 bc	0.46 c	0.16 cd	0.61 de	1.23 d
–Mg	17.4 abc	91 a	8.2 abc	0.89 b	0.19 cd	0.66 de	1.74 cd
–S	8.6 bc	84 a	10.0 ab	0.70 bc	0.24 bc	1.32 bc	2.26 bc

[1] Height growth is the difference in heights between the time deficiency treatments were begun and harvest.

[2] Values followed by the same letter in a column are not significantly different (0.05 level) using Duncan's New Multiple Range Test.

[3] Total seedling height measured from the root collar to the top of the terminal bud.

Table 29.—*Average height growth, stem height, number of leaves, ovendry weight of foliage, stem, and root of red maple seedlings after 117 days under deficiency treatments*

Treatment	Height growth[1]	Height[3]	Number of leaves	Average dry weight per seedling			
				Foliage	Stem	Root	Total
	........mm	....		....................gms	....		
Complete	154.4 ab[2]	227 ab	19.2 ab	1.78 a	1.14 a	2.91 a	5.83 a
D-H_2O	1.0 d	77 d	7.6 d	0.13 d	0.10 de	0.27 c	0.50 d
-N	163.0 a	232 a	18.8 ab	0.95 b	0.77 abc	1.27 bc	2.99 bc
-P	22.6 cd	91 cd	9.6 cd	0.17 cd	0.09 e	0.26 c	0.52 d
-K	60.2 cd	136 cd	14.4 bc	0.76 bcd	0.24 de	0.45 c	1.45 cd
-Ca	37.2 cd	115 cd	12.8 cd	0.45 bcd	0.27 cde	0.71 bc	1.47 cd
-Mg	222.0 a	297 a	22.0 a	2.13 a	1.01 ab	1.41 b	4.55 ab
-S	79.2 c	153 cd	12.6 cd	0.80 bc	0.60 bcd	1.62 b	3.02 bc

[1] Height growth is the difference in heights between the time deficiency treatments were begun and harvest.

[2] Values followed by the same letter in a column are not significantly different (0.05 level) using Duncan's New Multiple Range Test.

[3] Total seedling height measured from the root collar to the top of the terminal bud.

able 30.—*Average height growth, stem height, number of leaves, ovendry weight of foliage, stem, and root of white ash seedlings after 113 days under deficiency treatments*

reatment	Height growth[1]	Height[3]	Number of leaves	Average dry weight per seedling			
				Foliage	Stem	Root	Total
	........mm	....		....................gms	....		
omplete	62 bcd[2]	156 bcd	10.4 ab	0.69 a	0.51 a	2.30 a	3.51 ab
-H_2O	39 cd	120 cd	7.2 c	0.24 b	0.17 b	0.70 c	1.11 cd
-N	28 d	128 cd	8.4 bc	0.32 b	0.20 b	0.81 c	1.33 d
-P	68 bc	167 abcd	9.6 bc	0.57 a	0.50 a	2.07 a	3.14 ab
-K	79 b	168 abc	10.6 ab	0.70 a	0.55 a	2.35 a	3.59 a
-Ca	56 bcd	149 bcd	9.4 bc	0.49 ab	0.39 ab	0.91 bc	1.79 bcd
-Mg	117 a	209 a	12.8 a	0.82 a	0.62 a	1.97 ab	3.41 ab
-	83 ab	194 ab	10.8 ab	0.64 a	0.50 a	1.48 abc	2.62 abcd

Height growth is the difference in heights between the time deficiency treatments were begun and harvest.

Values followed by the same letter in a column are not significantly different (0.05 level) using Duncan's New Multiple Range Test.

Total seedling height measured from the root collar to the top of the terminal bud.

Table 31.— Average height growth, stem height, number of leaves, ovendry weight of foliage, stem, and r
of paper birch seedlings after 113 days under deficiency treatments

Treatment	Height growth[1]	Height[3]	Number of leaves	Average dry weight per seedling Foliage	Stem	Root	Total
	........*mm*	....		....	....*gms*	....	....
Complete	179 ab[2]	202 ab	25.5 ab	1.65 b	.66 b	2.28 b	4.59 b
D–H_2O	10 e	35 e	9.4 d	.14 f	.05 d	.16 d	.35 d
–N	17 e	42 e	8.8 d	.17 f	.05 d	.18 d	.40 d
–P	100 cd	125 cd	21.6 bc	.62 e	.35 c	.91 c	1.88 c
–K	171 ab	193 ab	31.6 c	1.61 bc	.75 b	2.43 b	4.78 b
–Ca	69 d	95 d	17.6 c	1.01 de	.32 c	1.10 c	2.43 c
–Mg	191 a	213 a	34.2 a	1.38 cd	.47 bc	1.17 c	3.02 c
–S	128 bc	155 bc	26.6 ab	1.15 d	.55 bc	1.18 c	2.88 c

[1] Height growth is the difference in heights between the time deficiency treatments were begun and harvest.

[2] Values followed by the same letter in a column are not significantly different (0.05 level) using Duncan's New Multiple Range Test.

[3] Total seedling height measured from the root collar to the top of the terminal bud.

Erdmann, Gayne G., Frederick T. Metzger, and Robert R. Oberg.
1979. Macronutrient deficiency symptoms in seedlings of four northern hardwoods. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-53, 36 p. U.S. Dep. Agric. For. Serv., North Cent. For. Exp. Stn., St. Paul, MN.

Illustrates and describes the visual deficiency symptoms for N, P, K, Ca, Mg, and S in sugar maple, red maple, white ash, and paper birch seedlings. Effects of these deficiencies on the development and nutrient composition of seedlings are also examined.

OXFORD: 424.7. KEY WORDS: (*Acer saccharum* Marsh.), (*Acer rubrum* L.), (*Fraxinus americana* L.), (*Betula papyrifera* Marsh.), chemical composition of tissues, dry-matter production, seedling development.

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Metric site index curves for aspen, birch and conifer in the Lake States

Paul R. Laidly

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Aspen
Birch
Conifer
PROGRAM REPORT

orth Central Forest Experiment Station, Forest Service, U.S. Department of Agriculture

This paper is a contribution from the Aspen-Birch-Conifer Program. The Aspen-Birch-Conifer Program is a coordinated, multi-disciplinary research effort. Its mission is to increase and integrate knowledge of the aspen-birch-conifer forests of the northern Great Lakes region in order to better identify and evaluate resource management alternatives.

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1979

METRIC SITE INDEX CURVES FOR ASPEN, BIRCH, AND CONIFERS IN THE LAKE STATES

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Grand Rapids, Minnesota

"It is therefore declared that the policy of the United States shall be to coordinate and plan the increasing use of the metric system in the United States . . ."[1]

Site index is the measured or estimated height of dominant and codominant trees at age 50. It is widely used both as an indicator of potential site productivity and as the basis for silvicultural recommendations for Lake States timber species. The manager's handbooks for aspen (Perala 1977), black spruce (Johnston 1977a), and northern white-cedar (Johnston 1977b) require an estimate of site index to use their "Key for Recommendations". Yield tables for all Lake States timber species require an estimate of site index. Also, site index curves have been used to estimate mean height growth of dominant and codominant trees because they are actually cumulative height curves.

Lundgren and Dolid (1970) recognized both the potential error in interpolating between curves and the need to facilitate electronic data processing of information that required an estimate of height or site index. They provided mathematical functions describing published site index curves for 11 Lake States timber species. The purpose of this paper is to complement their work by providing site index equations, curves, and height tables in metric units.

EQUATIONS

Lundgren and Dolid (1970) described published site index curves as:

$$H = b_1 S (1 - e^{b_2 A})^{b_3}$$

where H = total height of trees in feet,
S = site index (height at age 50 years),
A = age in years,
e = base of the natural logarithm,
and b_1, b_2, and b_3 are estimated parameters.

From this equation, site index (S) is linearly related to height (H) at any given age. And H, in meters, can be estimated by expressing S as height in meters at age 50. Therefore, the parameter estimates published by Lundgren and Dolid (1970) are valid for estimating height in meters if site index is also expressed in meters (table 1). (Site index in feet can be converted to site index in meters by multiplying by 0.3048 meters per foot.)

CURVES AND TABLES

The site index curves (figs. 1-9) and height tables (tables 2-10) were produced from the equations in table 1. To facilitate the transfer from feet to meters, the metric site index curves illustrated in figures 1-9 were chosen to correspond as closely as possible to the published site index curves in feet. Tables 2-10 are provided so interpolation between curves is not necessary.

USE AND LIMITATIONS

Several dominant and codominant trees should be measured for height and age to estimate site index. The number of sample trees will depend on the range of heights and ages in the stand. Gevorkiantz (1956) gives a rule-of-thumb for an adequate sample as:

$$n = 5 + R^2/30$$

---

[1] *Metric Conversion Act of 1975, Public Law 94-168.*

where R = observed range of heights or ages in the stand.

Site index cannot be properly evaluated if dominant and codominant trees have been affected by suppression or fire— aspen site index can be underestimated as much as 3 to 5 meters in stands with a fire history (Stoeckeler 1960). Site index curves should not be used in extremely dense, stagnated stands; in very open stands with excessive crown development; or in stands where the height growth of dominant and codominant trees deviates widely from the trend illustrated by the curves (such as in stands that have developed under uncommon soil or climatic conditions). Also, care must be exercised when estimating site index in young stands. Site index is the mean tree height of dominants and codominants at a specific point in time. Therefore, site index does not change with time. But, it is not uncommon for the estimate of site index to change from one measurement to another, particularly if the estimates are made when the stand is less than 30 years old.

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Table 1.—*Parameters of the equation describing metric site index curves*[1] (derived from Lundgren and Dolid 1970)

Species	Parameters			Standard error	Maximum error
	b_1	b_2	b_3		
				-------meters------	
Red pine	1.890	−0.01979	1.3892	.19	.43
Jack pine	1.633	−0.02233	1.2419	.15	.34
White pine	1.966	−0.02399	1.8942	.20	.52
Balsam fir	1.437	−0.02266	0.9381	.21	.58
Black spruce	1.762	−0.02011	1.2307	.22	.58
Tamarack	1.547	−0.02246	1.1129	.16	.43
Northern white-cedar	1.973	−0.01535	1.0895	.20	.52
Aspen	1.480	−0.02140	0.9377	.12	.34
Paper birch	1.598	−0.01938	0.9824	.10	.18

[1] Height = b_1 (Site Index (meters)) $(1-e^{b_2 (\text{Age})})^{b_3}$.

Table 2.— *Red pine height as related to site index and age*
(In meters)

Site	Age (years)										
index	20	30	40	50	60	70	80	90	100	110	120
10	4.0	6.2	8.2	9.9	11.4	12.7	13.7	14.6	15.4	16.0	16.5
11	4.4	6.8	9.0	10.9	12.5	13.9	15.1	16.1	16.9	17.6	18.2
12	4.8	7.4	9.8	11.9	13.7	15.2	16.5	17.6	18.4	19.2	19.8
13	5.2	8.0	10.6	12.9	14.8	16.5	17.9	19.0	20.0	20.8	21.5
14	5.6	8.7	11.4	13.9	16.0	17.7	19.2	20.5	21.5	22.4	23.1
15	6.0	9.3	12.3	14.9	17.1	19.0	20.6	21.9	23.1	24.0	24.8
16	6.4	9.9	13.1	15.9	18.2	20.3	22.0	23.4	24.6	25.6	26.4
17	6.8	10.5	13.9	16.8	19.4	21.5	23.3	24.9	26.1	27.2	28.1
18	7.2	11.1	14.7	17.8	20.5	22.8	24.7	26.3	27.7	28.8	29.7
19	7.6	11.8	15.5	18.8	21.7	24.1	26.1	27.8	29.2	30.4	31.4
20	8.0	12.4	16.3	19.8	22.8	25.3	27.5	29.3	30.7	32.0	33.0
21	8.4	13.0	17.2	20.8	23.9	26.6	28.8	30.7	32.3	33.6	34.7
22	8.8	13.6	18.0	21.8	25.1	27.9	30.2	32.2	33.8	35.2	36.3
23	9.2	14.2	18.8	22.8	26.2	29.1	31.6	33.6	35.4	36.8	38.0
4	9.6	14.9	19.6	23.8	27.4	30.4	33.0	35.1	36.9	38.4	39.6
5	10.0	15.5	20.4	24.8	28.5	31.7	34.3	36.6	38.4	40.0	41.3

Table 3.—*Jack pine height as related to site index and age*
(In meters)

Se	Age (years)								
i ex	20	30	40	50	60	70	80	90	100
	4.1	6.0	7.6	9.0	10.1	11.0	11.7	12.3	12.8
10	4.6	6.7	8.5	10.0	11.2	12.2	13.0	13.7	14.2
1	5.1	7.4	9.3	11.0	12.3	13.4	14.3	15.0	15.6
12	5.5	8.0	10.2	12.0	13.4	14.6	15.6	16.4	17.0
13	6.0	8.7	11.0	13.0	14.6	15.9	16.9	17.8	18.4
14	6.4	9.4	11.9	14.0	15.7	17.1	18.2	19.1	19.9
15	6.9	10.1	12.7	15.0	16.8	18.3	19.5	20.5	21.3
16	7.4	10.7	13.6	16.0	17.9	19.5	20.8	21.9	22.7
17	7.8	11.4	14.4	17.0	19.0	20.7	22.1	23.2	24.1
18	8.3	12.1	15.3	18.0	20.2	22.0	23.4	24.6	25.5
19	8.7	12.7	16.1	19.0	21.3	23.2	24.7	25.9	27.0
20	9.2	13.4	17.0	20.0	22.4	24.4	26.0	27.3	28.4
21	9.6	14.1	17.8	21.0	23.5	25.6	27.3	28.7	29.8
22	10.1	14.7	18.7	22.0	24.6	26.8	28.6	30.0	31.2

Table 4.—*White pine height as related to site index and age*
(In meters)

Site	Age (years)										
index	**20**	**30**	**40**	**50**	**60**	**70**	**80**	**90**	**100**	**110**	**120**
10	3.2	5.6	7.9	10.0	11.8	13.3	14.6	15.6	16.4	17.1	17.6
11	3.5	6.1	8.7	11.0	13.0	14.6	16.0	17.1	18.1	18.8	19.4
12	3.8	6.7	9.5	12.0	14.1	16.0	17.5	18.7	19.7	20.5	21.1
13	4.1	7.2	10.2	13.0	15.3	17.3	18.9	20.3	21.3	22.2	22.9
14	4.4	7.8	11.0	14.0	16.5	18.6	20.4	21.8	23.0	23.9	24.7
15	4.7	8.3	11.8	15.0	17.7	19.9	21.8	23.4	24.6	25.6	26.4
16	5.1	8.9	12.6	15.9	18.8	21.3	23.3	24.9	26.3	27.3	28.2
17	5.4	9.4	13.4	16.9	20.0	22.6	24.7	26.5	27.9	29.0	30.0
18	5.7	10.0	14.2	17.9	21.2	23.9	26.2	28.1	29.5	30.8	31.7
19	6.0	10.6	15.0	18.9	22.4	25.3	27.7	29.6	31.2	32.5	33.5
20	6.3	11.1	15.8	19.9	23.6	26.6	29.1	31.2	32.8	34.2	35.2
21	6.6	11.7	16.5	20.9	24.7	27.9	30.6	32.7	34.5	35.9	37.0
22	7.0	12.2	17.3	21.9	25.9	29.3	32.0	34.3	36.1	37.6	38.8
23	7.3	12.8	18.1	22.9	27.1	30.6	33.5	35.8	37.8	39.3	40.5
24	7.6	13.3	18.9	23.9	28.3	31.9	34.9	37.4	39.4	41.0	42.3
25	7.9	13.9	19.7	24.9	29.4	33.2	36.4	39.0	41.0	42.7	44.0

Table 5.—*Balsam fir height as related to site index and age*
(In meters)

Site	Breast height age (years)						
Index	**20**	**30**	**40**	**50**	**60**	**70**	**80**
9	5.0	6.7	8.0	9.0	9.8	10.4	10.9
10	5.6	7.4	8.8	10.0	10.9	11.6	12.2
11	6.1	8.1	9.7	11.0	12.0	12.8	13.4
12	6.7	8.9	10.6	12.0	13.1	13.9	14.6
13	7.2	9.6	11.5	13.0	14.1	15.1	15.8
14	7.8	10.4	12.4	14.0	15.2	16.2	17.0
15	8.4	11.1	13.3	15.0	16.3	17.4	18.2
16	8.9	11.8	14.1	16.0	17.4	18.5	19.5
17	9.5	12.6	15.0	17.0	18.5	19.7	20.7
18	10.0	13.3	15.9	18.0	19.6	20.9	21.9
19	10.6	14.1	16.8	19.0	20.7	22.0	23.1
20	11.1	14.8	17.7	20.0	21.8	23.2	24.3
21	11.7	15.6	18.6	21.0	22.8	24.3	25.5
22	12.3	16.3	19.5	22.0	23.9	25.5	26.7

Table 6.—*Black spruce height as related to site index and age*
(In meters)

Site index	Age (years)										
	20	30	40	50	60	70	80	90	100	110	120
6	2.7	4.0	5.1	6.0	6.8	7.5	8.0	8.5	8.9	9.2	9.4
7	3.2	4.7	5.9	7.0	8.0	8.7	9.4	9.9	10.3	10.7	11.0
8	3.6	5.3	6.8	8.0	9.1	10.0	10.7	11.3	11.8	12.2	12.6
9	4.1	6.0	7.6	9.1	10.2	11.2	12.0	12.7	13.3	13.7	14.1
10	4.5	6.6	8.5	10.1	11.4	12.5	13.4	14.1	14.8	15.3	15.7
11	5.0	7.3	9.3	11.1	12.5	13.7	14.7	15.6	16.2	16.8	17.3
12	5.4	8.0	10.2	12.1	13.7	15.0	16.1	17.0	17.7	18.3	18.8
13	5.9	8.6	11.0	13.1	14.8	16.2	17.4	18.4	19.2	19.9	20.4
14	6.3	9.3	11.9	14.1	15.9	17.5	18.7	19.8	20.7	21.4	22.0
15	6.8	10.0	12.7	15.1	17.1	18.7	20.1	21.2	22.1	22.9	23.5
16	7.2	10.6	13.6	16.1	18.2	20.0	21.4	22.6	23.6	24.4	25.1
17	7.7	11.3	14.4	17.1	19.3	21.2	22.8	24.0	25.1	26.0	26.7
18	8.1	12.0	15.3	18.1	20.5	22.5	24.1	25.5	26.6	27.5	28.3
19	8.6	12.6	16.1	19.1	21.6	23.7	25.4	26.9	28.1	29.0	29.8
20	9.0	13.3	17.0	20.1	22.8	24.9	26.8	28.3	29.5	30.6	31.4
21	9.5	14.0	17.8	21.1	23.9	26.2	28.1	29.7	31.0	32.1	33.0
22	9.9	14.6	18.7	22.1	25.0	27.4	29.4	31.1	32.5	33.6	34.5

Table 7.—*Tamarack height as related to site index and age*
(In meters)

Site index	Age (years)										
	20	30	40	50	60	70	80	90	100	110	120
6	3.0	4.2	5.2	6.0	6.6	7.2	7.6	7.9	8.2	8.4	8.6
7	3.5	4.9	6.1	7.0	7.7	8.4	8.9	9.2	9.6	9.8	10.0
8	4.0	5.6	6.9	8.0	8.9	9.6	10.1	10.6	10.9	11.2	11.4
9	4.5	6.3	7.8	9.0	10.0	10.7	11.4	11.9	12.3	12.6	12.9
10	5.0	7.0	8.6	10.0	11.1	11.9	12.6	13.2	13.7	14.0	14.3
11	5.5	7.7	9.5	11.0	12.2	13.1	13.9	14.5	15.0	15.4	15.7
12	6.0	8.4	10.4	12.0	13.3	14.3	15.2	15.8	16.4	16.8	17.2
13	6.5	9.1	11.2	13.0	14.4	15.5	16.4	17.2	17.8	18.2	18.6
14	7.0	9.8	12.1	14.0	15.5	16.7	17.7	18.5	19.1	19.6	20.0
15	7.5	10.5	13.0	15.0	16.6	17.9	19.0	19.8	20.5	21.0	21.5
16	8.0	11.2	13.8	16.0	17.7	19.1	20.2	21.1	21.9	22.4	22.9
17	8.5	11.9	14.7	17.0	18.8	20.3	21.5	22.5	23.2	23.8	24.3
18	9.0	12.6	15.6	18.0	19.9	21.5	22.8	23.8	24.6	25.2	25.8
19	9.5	13.3	16.4	19.0	21.0	22.7	24.0	25.1	26.0	26.6	27.2
20	10.0	14.0	17.3	20.0	22.1	23.9	25.3	26.4	27.3	28.0	28.6
21	10.5	14.7	18.2	21.0	23.2	25.1	26.6	27.7	28.7	29.4	30.1
22	11.0	15.4	19.0	22.0	24.3	26.3	27.8	29.1	30.1	30.8	31.5

Table 8.—*Northern white-cedar height as related to site index and age*
(In meters)

Site index	Age (years) 20	30	40	50	60	70	80	90	10
6	2.8	4.0	5.1	6.0	6.8	7.5	8.1	8.6	9.
7	3.2	4.7	5.9	7.0	7.9	8.8	9.5	10.1	10.
8	3.7	5.3	6.8	8.0	9.1	10.0	10.8	11.5	12.
9	4.2	6.0	7.5	9.0	10.2	11.3	12.2	13.0	13.
10	4.6	6.7	8.4	10.0	11.3	12.5	13.5	14.4	15.
11	5.1	7.3	9.3	11.0	12.5	13.8	14.9	15.8	16.
12	5.6	8.0	10.1	12.0	13.6	15.0	16.2	17.3	18.
13	6.0	8.7	11.0	13.0	14.8	16.3	17.6	18.7	19.
14	6.5	9.3	11.8	14.0	15.9	17.5	18.9	20.2	21.
15	6.9	10.0	12.7	15.0	17.0	18.8	20.3	21.6	22.
16	7.4	10.7	13.5	16.0	18.2	20.0	21.6	23.0	24.
17	7.9	11.3	14.4	17.0	19.3	21.3	23.0	24.5	25.
18	8.3	12.0	15.2	18.0	20.4	22.5	24.3	25.9	27.
19	8.8	12.7	16.0	19.0	21.6	23.8	25.7	27.4	28.
20	9.3	13.3	16.9	20.0	22.7	25.0	27.1	28.8	30.

Table 9.—*Aspen height as related to site index and age*
(In meters)

Site Index	Age (years) 20	30	40	50	60	70	8
11	6.1	8.1	9.7	11.0	12.0	12.8	13.
12	6.6	8.8	10.6	12.0	13.1	14.0	14.
13	7.2	9.5	11.5	13.0	14.2	15.2	16.
14	7.7	10.3	12.3	14.0	15.3	16.3	17.
15	8.3	11.0	13.2	15.0	16.4	17.5	18.
16	8.8	11.8	14.1	16.0	17.5	18.7	19.
17	9.4	12.5	15.0	17.0	18.6	19.8	20.
18	9.9	13.2	15.9	18.0	19.7	21.0	22.
19	10.5	14.0	16.7	19.0	20.7	22.2	23.
20	11.0	14.7	17.6	20.0	21.8	23.3	24.
21	11.6	15.4	18.5	21.0	22.9	24.5	25.
22	12.1	16.2	19.4	22.0	24.0	25.7	27.
23	12.7	16.9	20.3	23.0	25.1	26.8	28.
24	13.2	17.6	21.1	24.0	26.2	28.0	29.
25	13.8	18.4	22.0	25.0	27.3	29.2	30.

Table 10.—*Paper birch height as related to site index and age*
(In meters)

Site	**Age (years)**						
Index	**20**	**30**	**40**	**50**	**60**	**70**	**80**
11	5.8	7.9	9.6	11.0	12.2	13.1	13.9
12	6.3	8.6	10.5	12.0	13.3	14.3	15.2
13	6.8	9.3	11.3	13.0	14.4	15.5	16.4
14	7.3	10.0	12.2	14.0	15.5	16.7	17.7
15	7.9	10.7	13.1	15.0	16.6	17.9	19.0
16	8.4	11.4	13.9	16.0	17.7	19.1	20.2
17	8.9	12.2	14.8	17.0	18.8	20.3	21.5
18	9.4	12.9	15.7	18.0	19.9	21.5	22.8
19	10.0	13.6	16.6	19.0	21.0	22.7	24.0
20	10.5	14.3	17.4	20.0	22.1	23.9	25.3
21	11.0	15.0	18.3	21.0	23.2	25.0	26.5
22	11.5	15.7	19.2	22.0	24.3	26.2	27.8
23	12.0	16.4	20.0	23.0	25.4	27.4	29.1
24	12.6	17.2	20.9	24.0	26.5	28.6	30.3
25	13.1	17.9	21.8	25.0	27.6	29.8	31.6

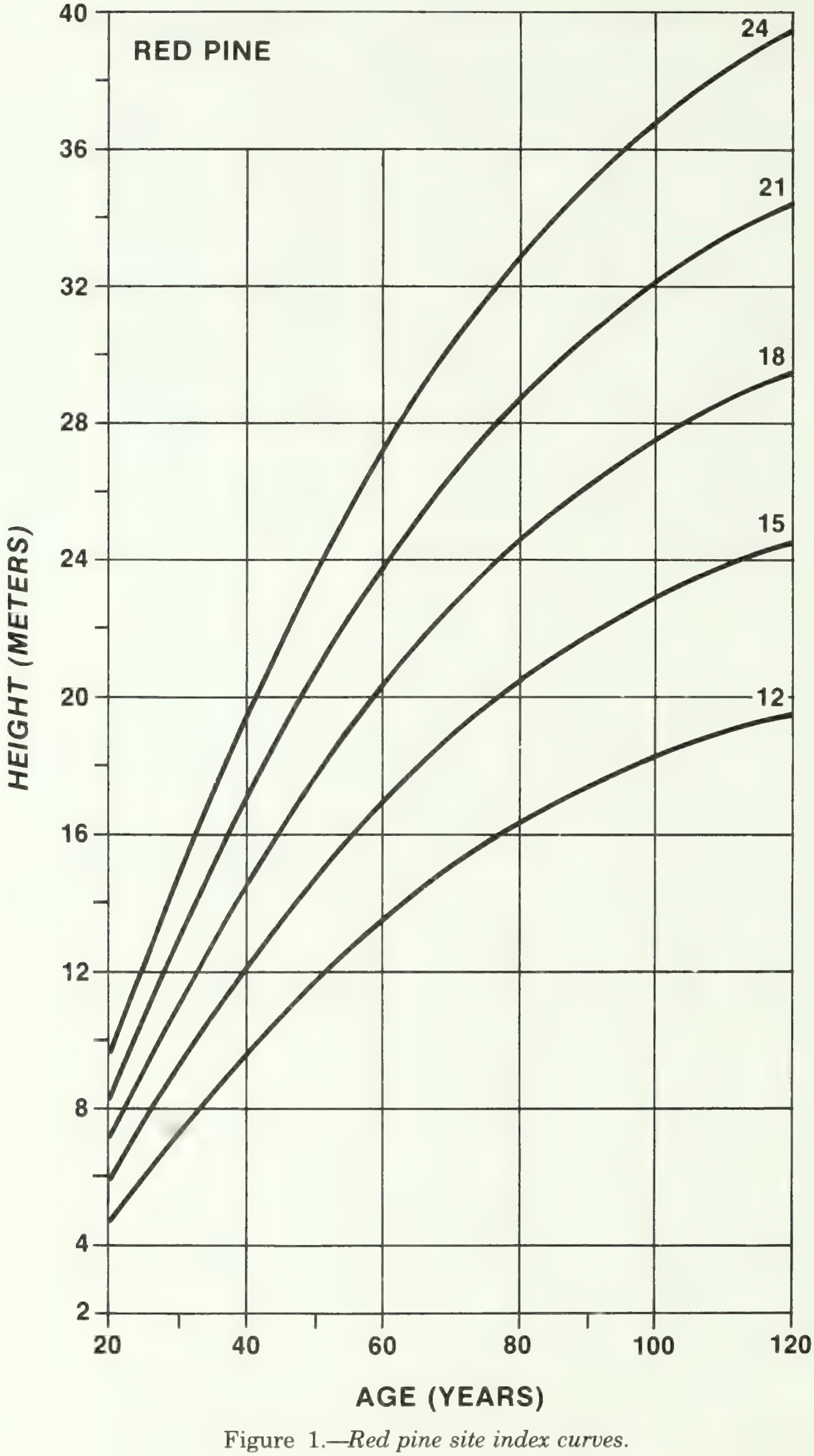

Figure 1.—*Red pine site index curves.*

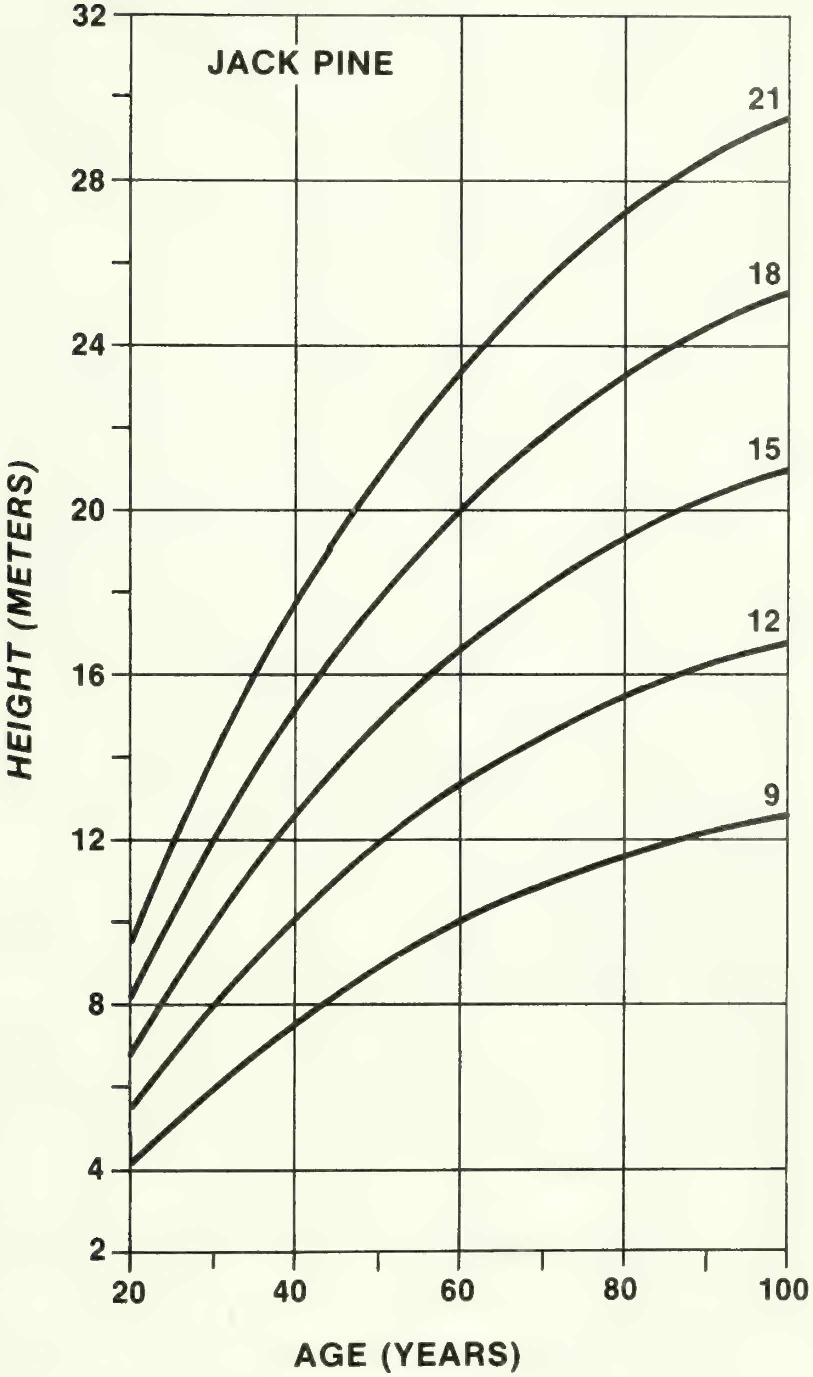

Figure 2.—*Jack pine site index curves.*

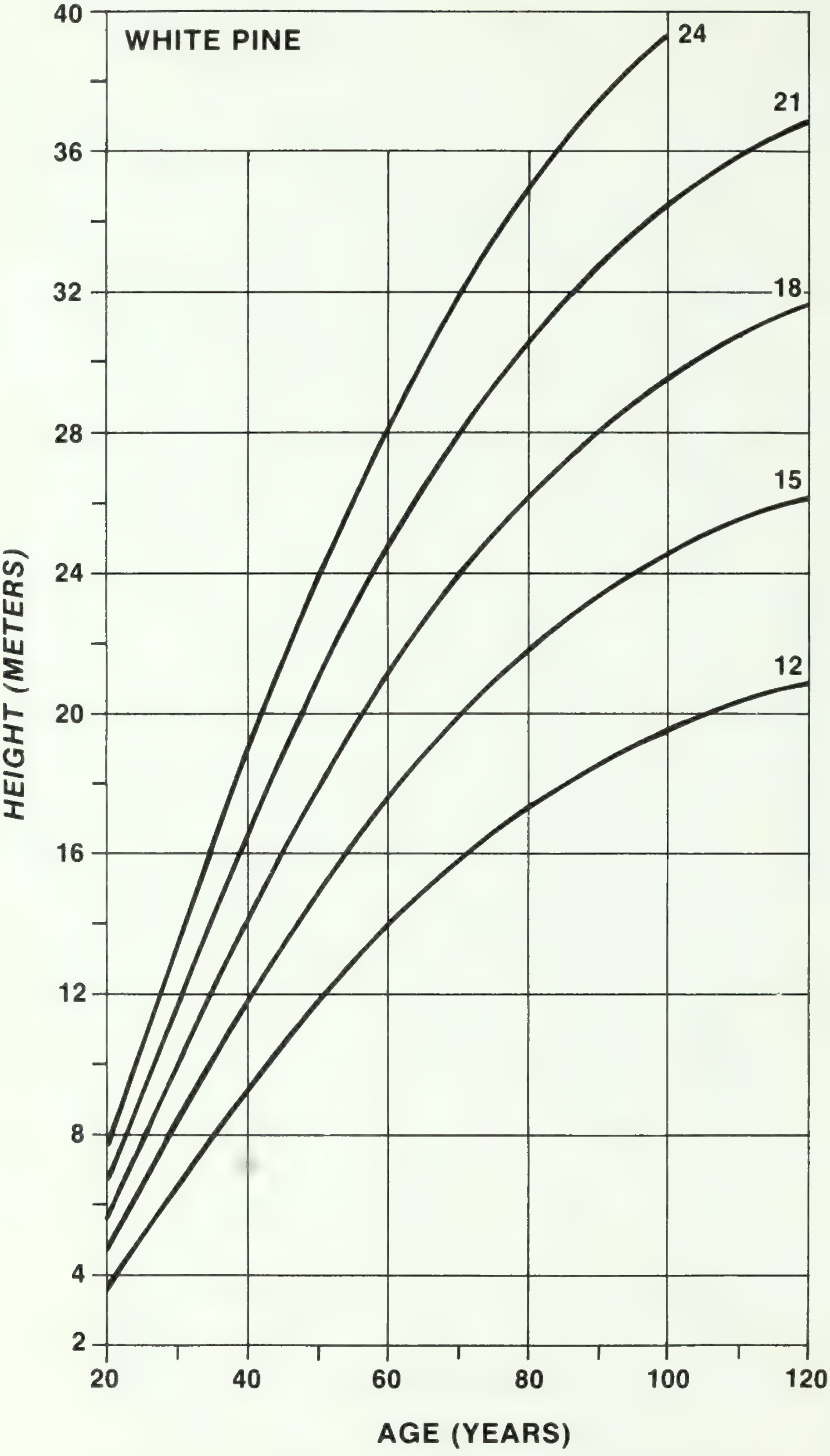

Figure 3.—*White pine site index curves.*

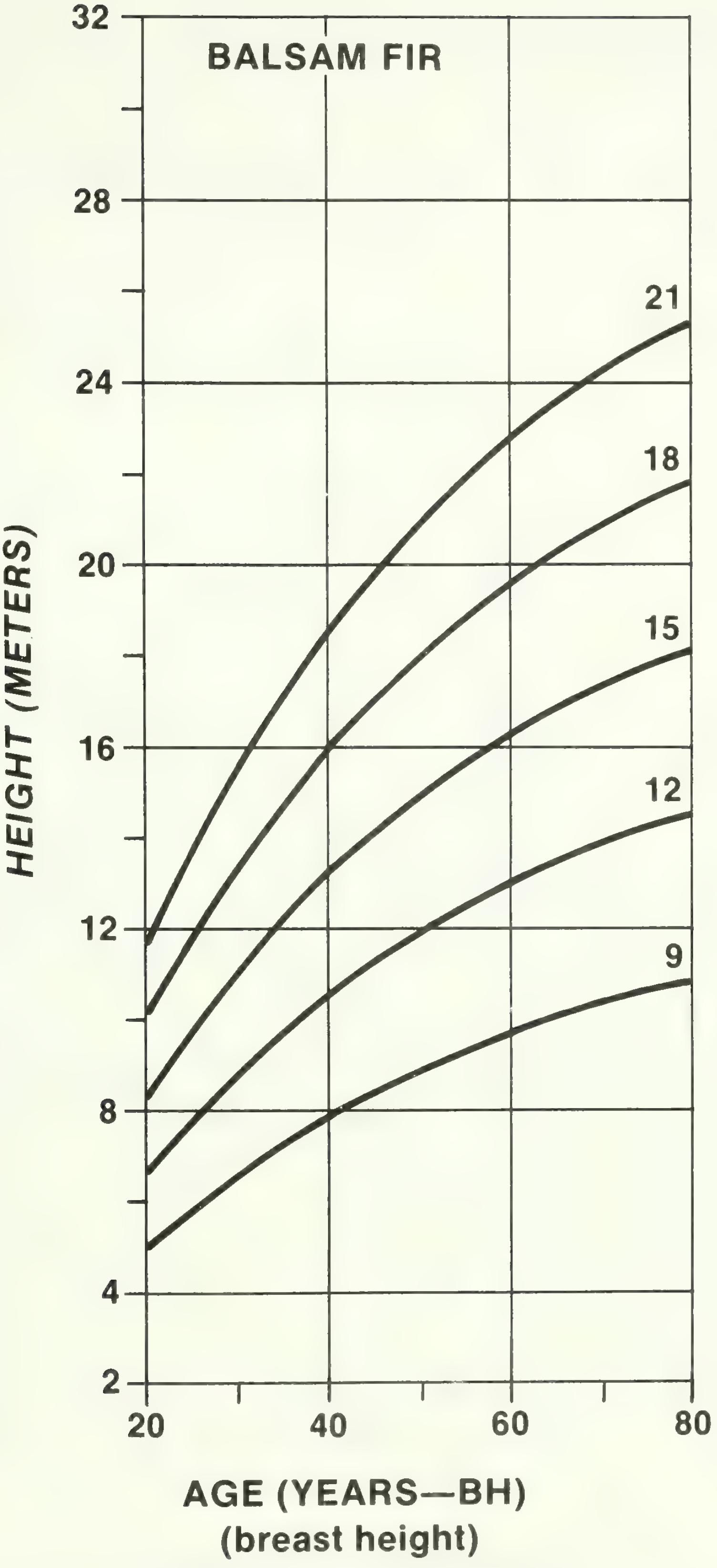

Figure 4.—*Balsam fir site index curves.*

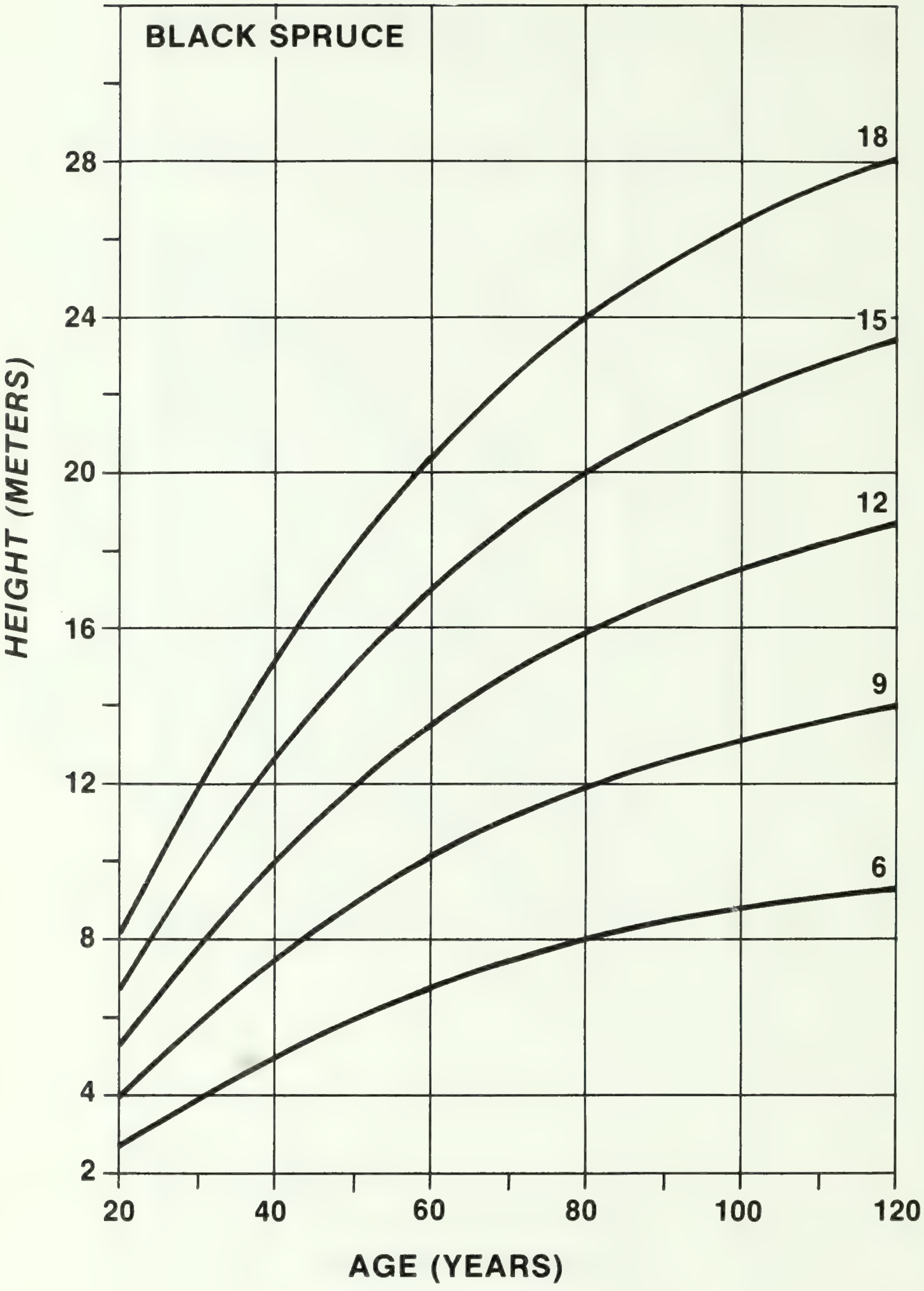

Figure 5.—*Black spruce site index curves.*

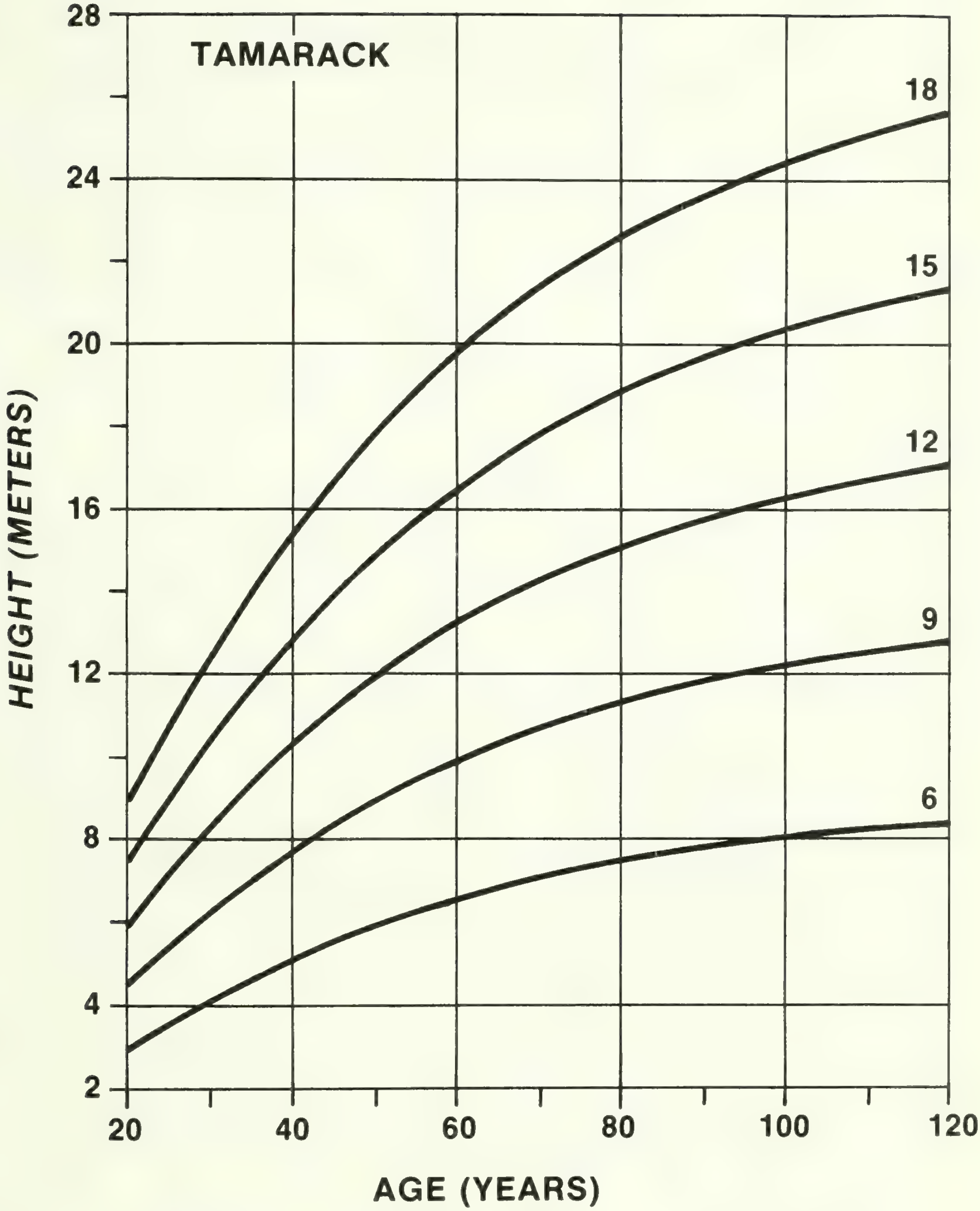

Figure 6.—*Tamarack site index curves.*

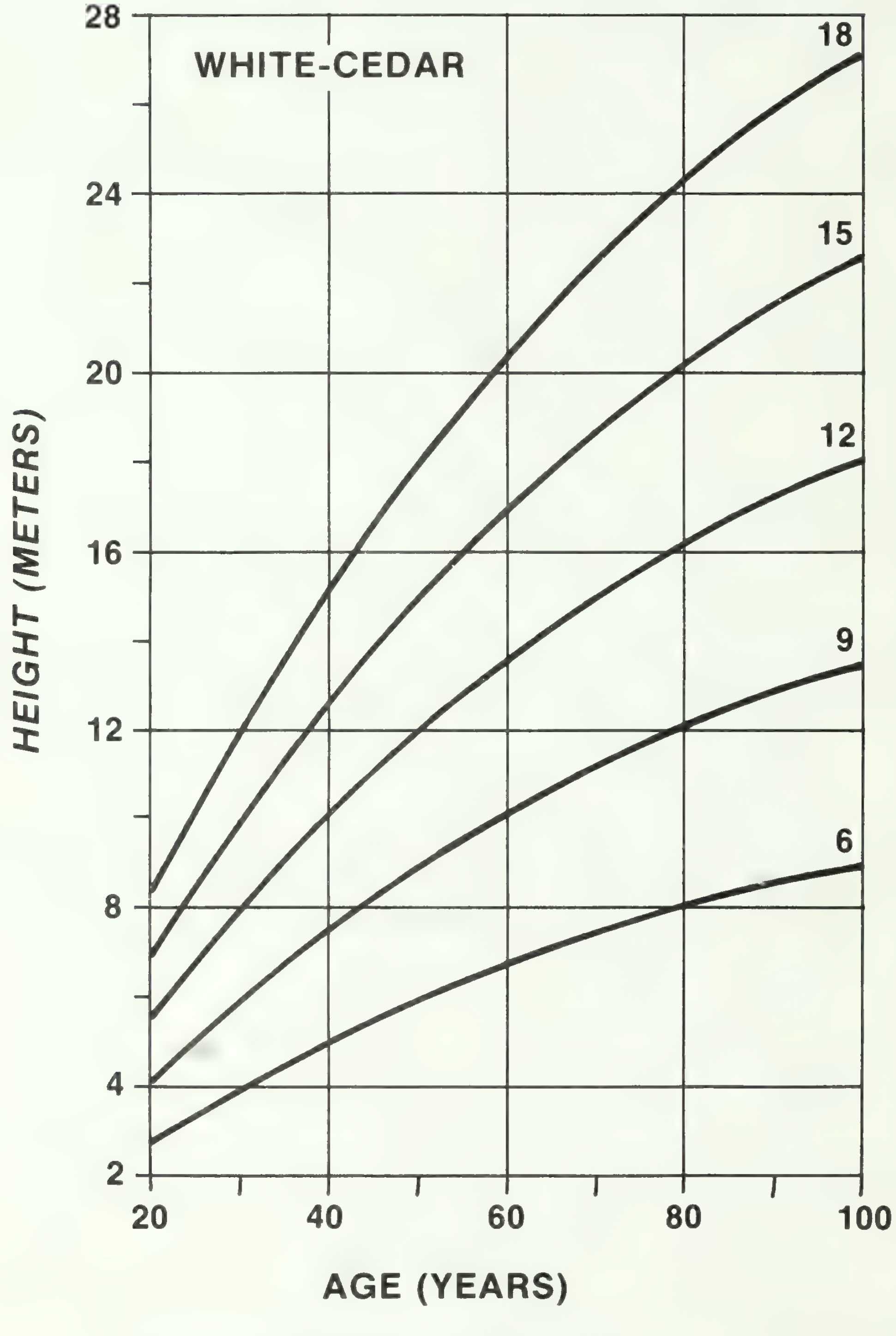

Figure 7.—*Northern white-cedar site index curves.*

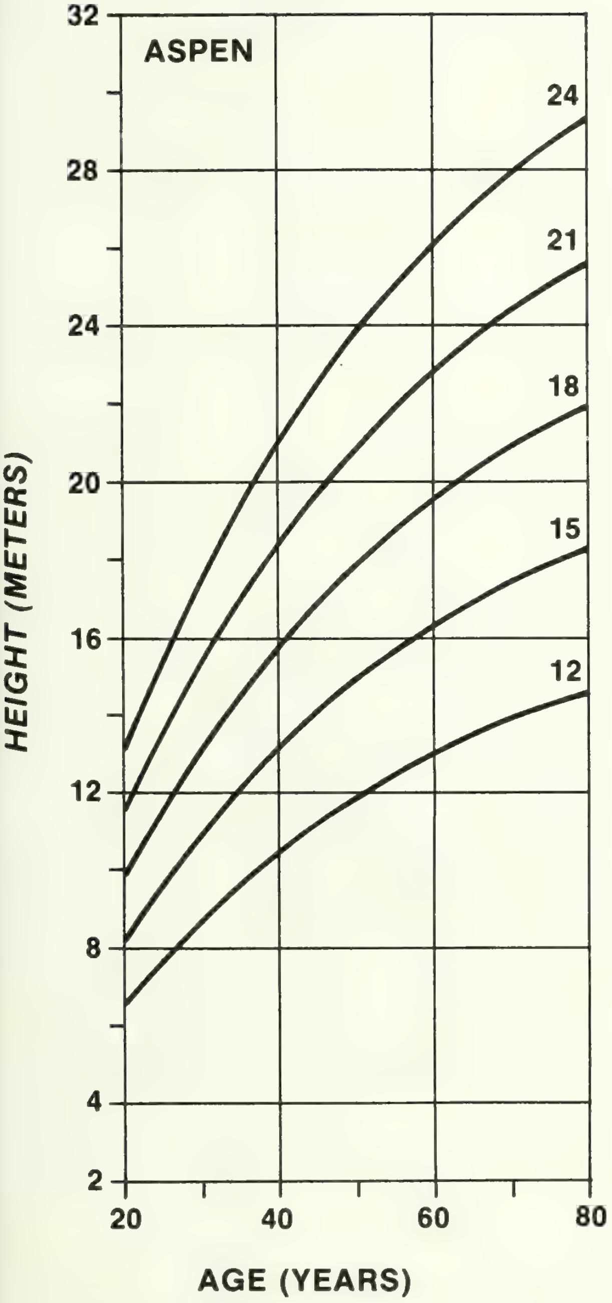

Figure 8.—*Aspen site index curves.*

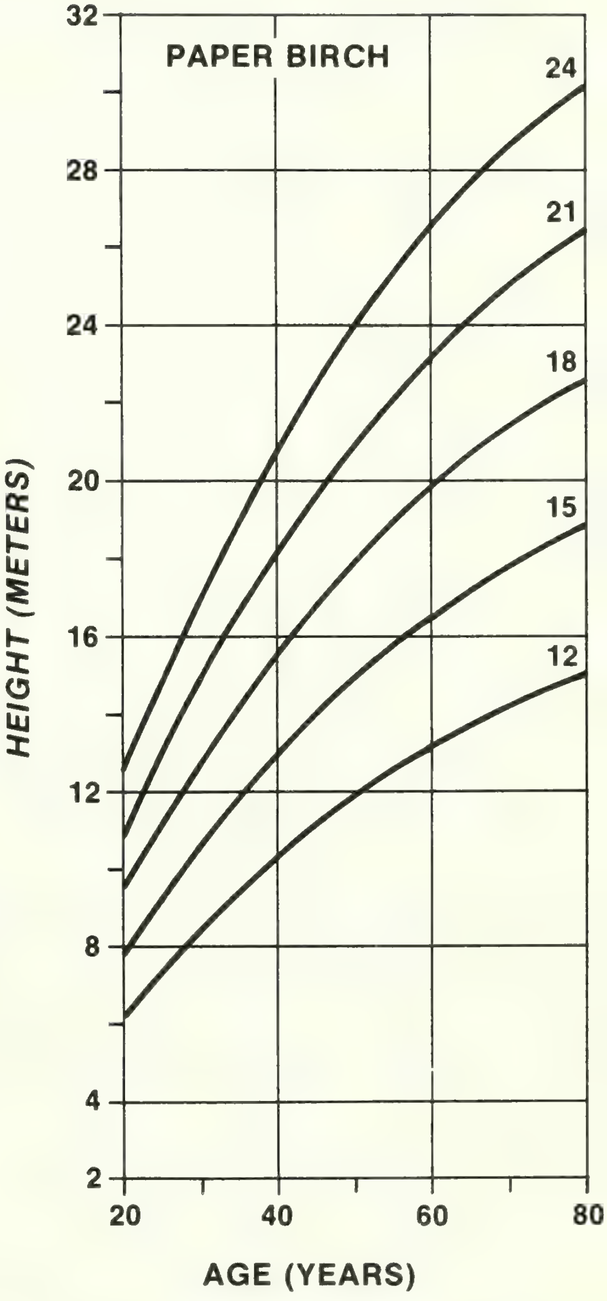

Figure 9.—*Paper birch site index curves.*

Laidly, Paul R.
1979. Metric site index curves for aspen, birch, and conifers in the Lake States. U.S. Dep. Agric. For. Serv., Gen. Tech. Rep. NC-54, 15 p. U.S. Dep. Agric. For. Serv., North Cent. For. Exp. Stn., St. Paul, MN.

Provides metric site index equations, tables, and curves for nine Lake States timber species.

OXFORD: 541(77). KEY WORDS: Red pine, white pine, jack pine, black spruce, tamarack, white-cedar, balsam fir.

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Man paints houses...
only nature should paint
trees and rocks.

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Determining fixed and operating cos
# of logging equipme

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DETERMINING FIXED AND OPERATING COSTS OF LOGGING EQUIPMENT

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During the past two decades, the declining supply of woods labor and rapidly increasing demand for, and cost of wood products have given impetus to the development of new logging equipment.

Today's logging equipment ranges anywhere from chain saws to complex multi-functional equipment which can fell, delimb, buck, and haul to the landing. To select specific equipment and use that equipment profitably, loggers should know something of equipment costs and how to determine them.

This paper analyzes equipment costs and gives a procedure for estimating them. It is intended for those who are in the logging business and need a standardized guide to help them appraise the efficiency and production costs of logging equipment. It can also be used as a basic teaching aid for forestry students.

PRELIMINARY DATA AND DEFINITIONS

Total equipment costs include all costs accrued from buying, owning, and operating equipment. For analysis, equipment costs can be grouped into **fixed costs, operating costs,** and **labor costs.** To calculate these costs, the user needs preliminary information and understanding of the following definitions.

Equipment Specifications

Model, type of equipment, net horsepower at flywheel, capacity of crankcase, and hours between oil changes, are necessary to calculate the cost of equipment per unit of time. They can be obtained from either the equipment specification sheet, the owner's manual, or both.

Initial Investment (P)

This is defined as the actual equipment purchase cost, less the tire cost, regardless of whether the equipment is purchased at full price or discounted rates.

The initial investment includes the following sub-categories:

- Equipment costs with standard attachment
- Optional attachment cost
- Sales taxes (State and local)
- Freight cost
- Miscellaneous

Freight costs are usually given in terms of F.O.B. free-on-board price. F.O.B. price simply means that at the given location the buyer takes title to the equipment and is responsible for shipment if necessary. The most common pricing policies are F.O.B. factory and F.O.B. delivered price (Ballau 1973):

- F.O.B. factory price—the buyer takes title to the equipment at the factory and is responsible for shipment.
- F.O.B. delivered price—the equipment is priced at a specific delivery point. The price includes freight, packing, insurance, etc., and the buyer takes title of the equipment at this point.

Miscellaneous costs, such as for installation or adaptation of the equipment to the logging system, should be included in the initial investment cost.

Salvage Value (S)

This is defined as the amount that equipment can be sold for at the time of its disposal. The actual salvage value of equipment is affected by current market demand for used equipment and the condition of the equipment at the time of disposal. However, estimating the future salvage value of equipment is very difficult because it is based on the future market value and the unknown condition of the equipment at the time of its disposal. The estimates come from owners themselves or from manufacturers or dealers. As a rule of thumb, the salvage value can be considered 20 percent of the initial investment cost.

Economic Life (N)

This is the period over which the equipment can operate at an acceptable operating cost and productivity. The economic life is generally measured in terms of years, hours, or mileages (trucks and trailers). It depends on two factors—physical and functional impairment.

Physical impairment is caused by normal equipment deterioration due to such factors as corrosion, chemical decomposition, or by wear and tear due to abrasion, shock, and impact. These may result from normal and proper usage, abusive and improper usage, age, inadequate or lack of maintenance, or severe environmental conditions. Functional impairment is when the equipment simply cannot meet the demand for expansion of operation and change of harvesting system or becomes economically or technologically obsolete.

The best indication of economic life of equipment is based on personal experience with similar equipment. According to Plummer,[1] ". . . equipment owners generally look at their 'down' time as a guide on when to trade. When the down time of a particular piece of equipment causes the entire logging system to lose time, they generally trade. Also, when the cost of lost production exceeds the cost of owning a new piece of equipment they trade". If such experience or a record is unavailable, the information can be obtained from manufacturers, trade organizations, or knowledgeable associations. The estimated life of certain types of equipment may be used to calculate the cost of equipment per unit of time as follows ([2,3]):

Equipment	*Years*
Chain saw-straight blade	1
Chain saw-bow blade	1
Big stick loader	5
Shortwood hydraulic loader	5
Longwood hydraulic loader	4
Uniloader	3
Front end loader	5
Skidder (cable)	3
Skidder (grapple)	3
Shortwood prehauler	4
Longwood prehauler	4
Feller-buncher	5
Chipper	5
Slasher	3

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[1] *Personal communication from Mr. Glenn M. Plummer, Harvesting Development Manager, Georgia Kraft Company, Rome, GA.*

[2] *Under southern U.S. conditions.*

[3] *Source: Machine cost and rates table–handout at 1978 Timber Harvesting Short Course, LSU/MSU Logging and Forestry Operations Center, Bay St. Louis, MS.*

Scheduled Operating Time (SH)

Scheduled operating time is the time during which equipment is scheduled to do productive work (Rolston 1968). The time during which a machine is on standby is not considered scheduled operating time. If a machine is being replaced by a spare, the scheduled operating time of the replaced machine ends when the replacement arrives on the job. The scheduled operating time of the replacement begins when it starts to move toward the job. Scheduled operating time is determined as follows:

If a piece of equipment is scheduled for use 8 hours a day and the possible estimated working days (subtracting weekends, holidays, bad weather days, etc.), are 250, then:

SH = 8 hrs./day × 250 days/yr. = 2,000 hrs./yr.

Productive Time (H)

Productive time is that part of scheduled operating time during which a machine actually operates (Rolston 1968). Only rarely would scheduled operating time and productive time be equal for logging equipment due to delays such as mechanical breakdowns, personnel, weather, etc. Productive time (H) divided by scheduled operating time times 100 is termed percent machine utilization. To estimate the productive time of equipment use the following utilization percents (^{2,3}):

Equipment	*Utilization* (Percent)
Chain saw-straight blade	50
Chain saw-bow blade	50
Big stick loader	90
Shortwood hydraulic loader	65
Longwood hydraulic loader	64
Uniloader	60
Front end loader	60
Cable skidder	67
Grapple skidder	67
Shortwood prehauler	64
Longwood prehauler	64
Feller-buncher	65
Chipper	75
Slasher	67

For example, suppose that a grapple skidder is scheduled for 2,000 operating hours per year. Then the estimated productive time per year is:

H = 2,000 hrs./yr. × 67% = 1,340 hrs./yr.

FIXED COSTS

Fixed costs do not vary with hours of operation. They are neither affected by the amount of equipment activity nor output and are incurred regardless of whether a piece of equipment is used or not. Fixed costs include **depreciation, interest, insurance,** and **taxes.**

Depreciation (D)

A piece of equipment loses its value with time and possesses only salvage value (or trade-in value) at the time of trade-in. The basic objective of the depreciation schedule is to recover the initial investment cost of equipment each year over its estimated economic life. The method for calculating depreciation is ordinarily determined by its planned or desired effect on profit and income taxes through the economic life of equipment. The three common methods generally used to compute depreciation are: (1) straight line, (2) declining balance, and (3) sum-of-the-year's-digits.

Straight line method

This assumes that the value of equipment decreases at a constant rate for each year of its economic life. The mathematical formula is:

$$D = \frac{P-S}{N}$$

Where: D = yearly depreciation charge

P = initial investment cost of equipment

S = salvage value

N = economic life in years

also, $DR = \frac{1}{N}$, where DR = depreciation rate per year.

Example 1.—Suppose a track-type feller-buncher costs $85,000 (F.O.B. delivered price). The economic life and salvage value are estimated as 5 years and $17,000, respectively. Then:

$$D = \frac{P-S}{N} = \frac{85{,}000-17{,}000}{5} = 13{,}600 \text{ per year}$$

$$DR = \frac{1}{N} = \frac{1}{5} = 0.20 \text{ or 20 percent per year.}$$

The depreciation charge for each year and the undepreciated value at the end of each year are as follows:

Year	*Depreciation Charge*	*Undepreciated Value*
	(Dollars)	
0	—	85,000
1	13,600	71,400
2	13,600	57,800
3	13,600	44,200
4	13,600	30,600
5	13,600	17,000

Declining balance method

This assumes that a piece of equipment does not depreciate at a constant rate, but at a higher rate during the early years and less toward the end of its economic life. Tax laws allow that the equipment owner may use a depreciation rate 2, 1½, or 1¼ times as great as the rate of the straight-line method (U.S. Department of Treasury, IRS 1978). Thus, for income tax purposes, this method is favored by some who desire higher write-off rates during the early years of ownership and lesser rates in the later years.

Example 2.— If, in the preceding equipment example, a rate of twice the straight-line depreciation rate, or 40 percent is used, then the depreciation for the first year is:

$$\$85{,}000 \times .40 = \$34{,}000$$

and the value of equipment at the end of the first year is:

$$\$85{,}000 - \$34{,}000 = \$51{,}000$$

The depreciation value for the second year is calculated by applying the 40 percent rate to the value of equipment at the end of the first year, and so on over the estimated life of the equipment, using the following tabulation:

Year	*Depreciation Charge*	*Undepreciated Value*
	(Dollars)	
0	—	85,000
1	34,000	51,000
2	20,400	30,600
3	12,240	18,360
4	7,344	11,016
5	4,406	6,610

The $6,610 undepreciated value at the end of the fifth year is the estimated salvage value. If the estimated salvage value and the actual salvage value came to a different amount, this differential balance is usually written off when the equipment is traded in or disposed of.

Sum-of-the-year's-digits method

This method assumes that the value of equipment decreases at a decreasing fraction each year. This is achieved by applying a different fraction each year to the cost less its salvage value. The denominators of all the fractions are the same, that is, the sum of the numbers of years of estimated life. Thus, with a piece of equipment having an estimated economic life of 5 years, the denominator of fraction is 15 (the sum of 1 + 2 + 3 + 4 + 5). The numerator of the fractions is the number of years used in sequence, beginning with the number of the estimated economic life and decrease each year in consecutive order. Thus, the numerator for the first year is 5, for the 2nd, 3rd, 4th, and 5th years are 4, 3, 2, and 1, respectively. The numerator for each year is then divided by the common denominator. In this case, for example, the depreciation in the first year is 5/15 of the initial investment cost less salvage value, in the 2nd, 3rd, 4th, and 5th year are $^{4}/_{15}$, $^{3}/_{15}$, $^{2}/_{15}$, and $^{1}/_{15}$ of the initial investment cost less salvage value, respectively. To illustrate these, consider the following example.

Example 3.— Use the preceding equipment example again. The amount to be depreciated over its economic life is:

$85,000 − $17,000 = $68,000

The denominator of fraction is:

1 + 2 + 3 + 4 + 5 = 15

The depreciation charge for the first year is:

$68,000 × $^{5}/_{15}$ = $22,667

The undepreciated value at the end of the first year is:

$85,000 − $22,667 = $62,333

Proceeding in this manner, the yearly depreciation charge and the undepreciated value at the end of each year can be calculated using the following tabulation:

Year	*Depreciation Charge*		*Undepreciated Value*
	(Dollars)		
0	—		85,000
1	68,000 × $^{5}/_{15}$ =	22,667	62,333
2	68,000 × $^{4}/_{15}$ =	18,133	44,200
3	68,000 × $^{3}/_{15}$ =	13,600	30,600
4	68,000 × $^{2}/_{15}$ =	9,067	21,533
5	68,000 × $^{1}/_{15}$ =	4,533	17,000

The three methods described above are best compared graphically (fig. 1). The declining balance and the sum-of-the-year's-digits methods have higher depreciation values during the early years, as compared with the straight-line method. These accelerated depreciation methods are generally used to maximize income tax savings in the early years of the economic life of equipment. On the other hand, the straight-line is not only the simplest method to calculate depreciation, but is generally the accepted method for estimating equipment cost per unit of time.

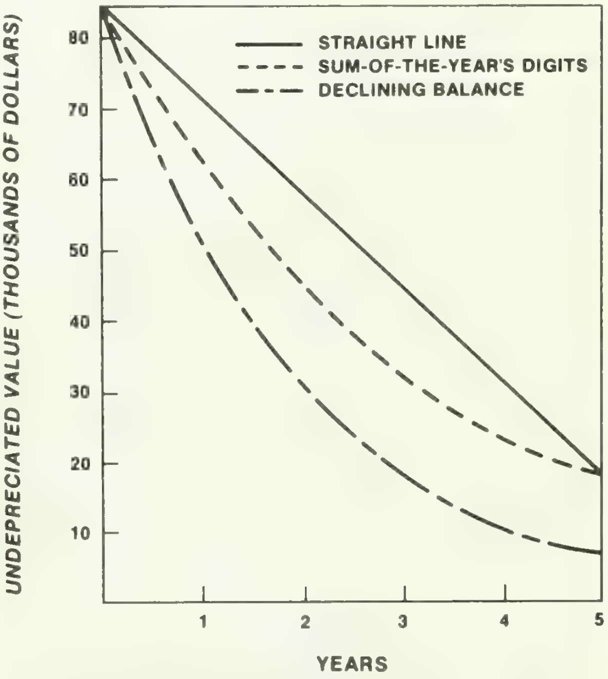

Figure 1.— *Graphical comparison of three methods.*

Interest, Insurance, and Taxes

Interest is the cost of using funds over a period of time. Investment funds may be borrowed or taken from savings or equity. If borrowed, the going interest rate is generally established by the lender. Interest rates may vary with locality and lending institution. If the money comes from personal savings or established equity, then an **opportunity cost,** or the rate this same money would earn if invested elsewhere (e.g., in U.S. savings bonds or a savings account), should be used as the interest rate. Twelve or 13 percent may be used as a rule of thumb for interest.

Every equipment owner must pay property or usage taxes on his equipment and should have one or more insurance policies for protection against damage, fire, and other destructive events. The cost of insurance and taxes also varies with locality and the type of equipment. Use the actual costs whenever they are available. If they are lacking, the Internal Revenue Service, the local court house, and insurance companies can provide some information concerning these costs. As a rule of thumb, 2 or 3 percent of the **average value of yearly investment** may be used for insurance, and 2 or 3 percent for taxes. The charges for interest, insurance, and taxes are generally applied to the average value of yearly investment. Two methods are usually used to calculate the average value of yearly investment (AVI).

The first method provides the average value of yearly investment over its entire economic life as follows:

$$AVI = \frac{(P-S)\,(N+1)}{2N} + S$$

Where: AVI = Average value of yearly investment over its entire economic life
P = Initial investment cost
S = Salvage value
N = Economic life in years.

Example 4.— Using the same equipment example, the charge for interest, insurance, and taxes are calculated as follows:

Data from Example 1 are:

Initial investment (P)	$85,000
Economic life (N)	5 years
Salvage value (S)(20% of P)	$17,000

Then,

Table 1.— *Charge for interest, insurance, and taxes*
(In dollars)

Charges and Investments	Year 1	2	3	4	5
Investment-year's start	85,000	62,333	44,200	30,600	21,533
Depreciation charge	22,667	18,133	13,600	9,067	4,533
Investment—year's end	62,333	44,200	30,600	21,533	17,000
Average yearly investment	73,667	53,267	37,400	26,067	19,267
Charge for interest, insurance and taxes (assume 18 percent)	13,260	9,588	6,732	4,692	3,468

$$\text{AVI} = \frac{(85{,}000-17{,}000)\ (5+1)}{2(5)} + 17{,}000 = \$57{,}800$$

per year

Now, assume the interest, insurance, and tax rate as 12, 3, and 3 percent, respectively. Then, total percentage of interest, insurance and taxes is:

$$12\% + 3\% + 3\% = 18\%$$

The charge for interest, insurance, and taxes is:

Total % × AVI = 18% × \$57,800 = \$10,404 per year.

The advantage of this method is simplicity. This method is generally used for estimating equipment cost for comparison with other equipment, or with the production cost (dollars per unit of output) of alternative equipment. (This formula is usable only if the straight-line method is used to calculate the depreciation) (see Appendix A).

The second method provides the average value of yearly investment for each year (Church 1978). The value of equipment does not decrease continually from initial investment to salvage value but drops in increments at the end of each year. The average value of yearly investment (AVI) equals investment at the beginning of the year divided by two.

Example 5.— To illustrate, we use the data from the sum-of-the-year's-digits method of depreciation (see tabulation, right column, page 5) as follows:

Investment cost (P) at the beginning of the first year	\$85,000
Depreciation charge for the first year	\$22,667
Investment cost (P) at the end of the first year	\$62,333

Then,

$$\text{AVI} = \frac{85{,}000+62{,}333}{2} = \$73{,}667 \text{ for the first year}$$

The charge for interest, insurance, and taxes (assuming 18 percent total) is:

18% × \$73,667 = \$13,260 for the first year.

Similarly, the charges for interest, insurance, and taxes are calculated over the estimated equipment life (table 1).

One advantage of this method is that interest, insurance, and taxes can be calculated for each year regardless of the method of the depreciation; another is that equipment costs can be estimated for long periods and the replacement time determined.

OPERATING COSTS

Operating costs, unlike fixed costs, change in proportion to hours of operation or use (fig. 2). They depend on a host of factors, many of which are under control of the operator or the equipment owner to a certain extent.

Maintenance and Repair

These include everything from simple maintenance to the periodic overhaul of engine, transmission, clutch, brakes, and other major equipment components. Storage costs and preventive maintenance are also included. Operator use or abuse of equipment, the severity of working conditions, maintenance and repair policies, and the basic equipment design and quality, all affect maintenance and repair costs.

The cost of periodically overhauling major components may be estimated from the owner's manual and the local cost of parts and labor, or by getting advice from the manufacturer. Another owner's experience with similar equipment and cost records under typical working conditions are valuable sources. If experienced owners or cost records are not available, the hourly maintenance and repair cost can be estimated as a percentage of hourly depreciation cost, from the following tabulation (Warren 1977):

Machine	*Percentage rate*
Crawler tractor	[4]100
Agricultural wheel tractor	[4]100
Rubber tired skidder (cable)	[4]50
Rubber tired skidder (hydraulic grapple)	60
Loader(cable)	30
Loader (hydraulic)[5]	50
Chain saw (include maintenance)	100
Feller-buncher	50

To estimate hourly maintenance and repair cost, multiply the percent rate by the depreciation cost and divide its product by productive time per year.

Example 6.— Using data from example 5:

Initial investment (P)	$85,000
Economic life (N)	5 years
Salvage value (S)	$17,000

Depreciation (straight-line method) =

$$\frac{85{,}000 - 17{,}000}{5} = \$13{,}600/\text{yr}.$$

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[4] *Including winch.*

[5] *Knuckleboom (stationary).*

From the tabulation above, the percent rate for a feller-buncher is 50 percent. So, maintenance and repair costs = 50% × 13,600 = \$6,800/yr.

Suppose the productive time has been established as 1,300 hours per year, then,

\$6,800/year ÷ 1,300 hours/year = \$5.23 per hour.

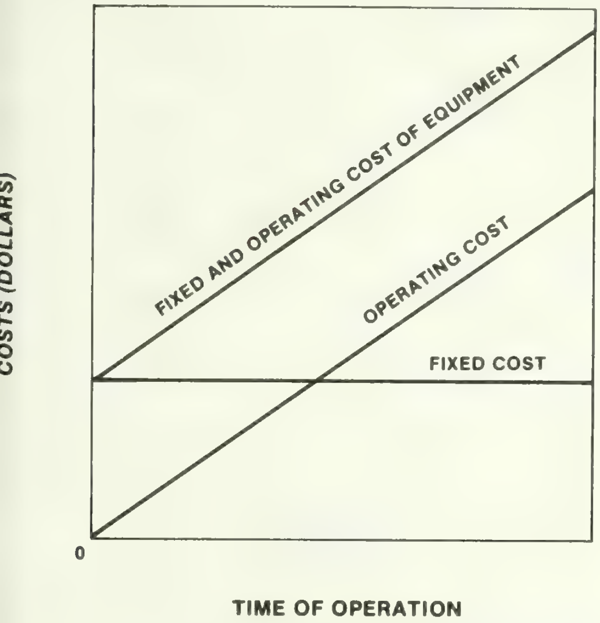

Figure 2.—*Nature of operating costs and fixed cost as a function of hours of operation and use.*

Fuel

The fuel consumption rate of a piece of equipment depends on the engine size, load factor, the condition of equipment, operator's driving habit, environmental conditions, and the basic design of equipment.

Determine the hourly fuel cost by dividing the total fuel cost by the productive time of that equipment.

If total fuel cost is not available, estimate hourly fuel cost (McCraw, 1963) as follows:

Fuel consumption rate for diesel engine:

$$\text{Gallons per hour} = \frac{0.40 \times 0.65}{7.08} \times \text{hp} = 0.037 \times \text{hp}$$

Fuel consumption rate for gasoline engine:

$$\text{Gallons per hour} = \frac{0.46 \times 0.65}{6.01} \times \text{hp} = 0.050 \times \text{hp}$$

Where: .40 = Pounds of diesel fuel consumed per hp hr. (FAO 1976)
.46 = Pounds of gasoline fuel consumed per hp hr. (FAO 1976)
.65 = The ratio of average net horsepower used to net hp available
hp = Net horsepower at rated maximum condition engine speed
7.08 = Weight (pound) of diesel fuel per gallon
6.01 = Weight (pound) of gasoline per gallon.

Then, calculate hourly fuel cost as follows:

For diesel engine:

Hourly fuel cost = 0.037 × hp × cost/gallon (local price)

For gasoline engine:

Hourly fuel cost = 0.050 × hp × cost/gallon (local price)

Example 7.— Suppose that a grapple skidder (diesel engine) has 150 hp and the local price of diesel fuel is \$.60 per gallon.

Then,

Hourly fuel cost = 0.037 × 150 × 0.60 = \$3.33

Lubricants

These include engine oil, transmission oil, final drive oil, hydraulic oil, grease, and filters. The consumption rate varies with the type of equipment, environmental working condition (temperature) the design of equipment, and the level of maintenance.

Derive hourly lubricant cost by dividing the total lubricant cost by the productive time.

If you lack actual data, estimate lubricant cost per hour (Peurifoy 1975) as follows:

$$Q = \text{hp} \times \frac{0.65 \times 0.006}{7.4} + \frac{c}{t}$$

Where: Q = Consumption rate (gallon/hour) of engine oil
hp = Net horsepower of engine
0.65 = Assume the ratio of average net horsepower used to net horsepower available.
0.006 = Pounds of engine oil consumed between oil changes per horsepower hour.
7.4 = Weight (pounds) of engine oil per gallon
c = Capacity of crank case, gallon
t = Number of hours between oil changes

Then, calculate hourly engine oil cost as follows:

Hourly engine oil cost =
(0.0005 × hp + c/t) × cost/gal. (local price)

Fifty percent of engine oil cost may be used for other lubricants (Peurifoy 1975).

Example 8.— Suppose that a grapple skidder has a 150 hp engine with a crankcase capacity of 5 gallons. The manufacturer recommends changing oil every 90 hours. The local price of oil is $2.00 per gallon. Then,

Hourly engine oil cost =
((0.0005 × 150) + 5/90) × $2.00 = $0.26
Hourly cost of other lubricants =
50% × 0.26 = $0.13.

Thus, the hourly cost of all lubricants for this skidder is the sum of 0.26 + 0.13.

Tires

Some cost analyses include tire cost in the initial investment cost. We consider tire cost part of the operating cost because of their shorter life. This cost is affected by the operator's driving habits, environmental and terrain conditions, wheel alignment, tire maintenance, and the local price.

The hourly tire cost is obtained by dividing the total tire cost (including tire and recaps) and maintenance by the total life of tire and recaps.

Suppose $1,000 for new tires, $500 for recaps, and $400 for tire maintenance and replacement including labor are spent for a rubber-tire skidder in a year. Productive time for skidder is 1340 hours per year. Then,

$$\text{Hourly tire cost} = \frac{1{,}000 + 500 + 400}{1{,}340} = \$1.42$$

If data are not available, the hourly tire cost may be estimated as follows (Jarck 1965):

$$\text{Hourly tire cost} = \frac{1.15\ (\text{tire cost})}{\text{tire life}}$$

Where: 1.15 = 1 + .15 (or 15%) the 15 percent addition to tire cost is for labor to repair or replace a malfunctioning tire.
Tire cost—obtained from manufacturers or local tire dealers.
Tire life—obtained from manufacturers or local tire dealers. One manufacturer suggests 3,000 hours for skidder type equipment and 4,000 hours for feller-bunch type equipment.

Example 9.—Suppose that a contractor selects tires for his rubber-tire grapple skidder and pays $7,000 for four tires. Then,

$$\text{Hourly tires cost} = \frac{1.15\ (7{,}000)}{3.000} = \$2.68$$

LABOR COST

Labor cost is the cost to keep an operator on the job; it may be on an hourly basis, a per unit of output basis,[6] or a combination of both. An employer must also contribute to Social Security, Federal Unemployment Insurance, State Unemployment Insurance, Workmen's Compensation, and other programs.

Social Security

This provides benefits for retirement, survivors, disability, and hospital insurance. For 1978, an employee pays 6.05 (6.13)[7] percent of the first $17,700 ($22,900) of his annual gross earnings and an employer matches this amount (U.S. Department of Treasury, IRS 1978). More information can be obtained from the Internal Revenue Service Office.

Federal Unemployment Insurance

Under law, an employer is subject to contribute if he employs one or more persons for any part of a day during each of 20 different calendar weeks or pays wages of $1,500 or more in any calendar quarter. For 1978, the rate is 3.4 percent on the first $6,000 of wages paid to each employee during the calendar year. A credit of 2.7 percent is given for contribution to State Unemployment Insurance and can be subtracted from the base federal rate of 3.4 percent (U.S. Department of Treasury, IRS 1978).

State Unemployment Insurance

The rates vary from State to State. The range is from 1.4 percent (Mississippi) to 2.8 percent (Maine) (APA 1977). More information can be obtained from the State Employment Security Agency and the State Insurance Commission.

Workmen's Compensation

Workmen's compensation provides protection for an employee against occupational hazards and benefits for his family to offset diminishing income resulting from injury on the job and work-related illness. The rate of workmen's compensation and benefits for employees vary from state to state. In logging or lumbering (transportation of logs to mill, construction, operation, logging railroads, or driving), the rates ranged from $10.20 per hundred dollars of payroll (North Carolina) to $55.52 per hundred dollars of payroll (Kentucky) (Hensel 1977). The Employers Insurance of Wausau, the State Employment Security Agency and the State Insurance Commission can provide more information.

Others

Other employer contributions may include paid vacation, paid holidays, paid sick leave, health insurance, uniforms, safety equipment, etc. The items and the rates vary greatly with locality and employers.

Labor cost is generally considered an operating cost. However, most operators stay in the woods and do minor repairs when the machines are down. Most of the time the wages are paid on a scheduled operating time basis. In this paper, labor cost is calculated on the scheduled operating time and is separated from fixed and operating cost. In this way, we can separate the cost of the machine itself from labor cost which varies greatly with locality and employers.

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[6] *The employer must pay minimum wages, even on per unit of output.*

[7] *Figures in parentheses are for 1979, based on personal contact with Internal Revenue Service personnel.*

ESTIMATING TOTAL EQUIPMENT COST

Two examples of estimating costs for logging follow. (A sample work sheet for calculating total equipment cost per unit of time is presented in Appendix B.)

Example 10.— A logger buys a shortwood front end loader costing $40,000 (F.O.B. delivered price). What are the hourly equipment costs? Assume the following:

Preliminary Data and Determinations

- Description of equipment—diesel, 80 hp net, 4 gallons of crankcase capacity, 80 hours between oil changes, track type.
- Diesel fuel, $.60/gallon.
- Engine oil, $2.00/gallon.
- Interest rate 12%, insurance 3%, taxes 3%.
- Labor cost, $7.00/hour (include the employer's contribution), based on scheduled operating time.
- Initial investment cost (P) $40,000
- Salvage value (S) (20% of P) $8,000
- Economic life (N) 5 years
- Scheduled operating time (SH) 2,000 hr/yr (8 hrs./day, 250 working days)
- Utilization (see tabulation, page 3) 65%
- Productive time (H) (2,000 × 65%) 1,300 hr/yr

Fixed cost

- Depreciation (D) = $\frac{P-S}{N} = \frac{40{,}000-8{,}000}{5 \text{ yrs}}$ = $ 6,400/yr
- Interest, insurance, and taxes 18% × AVI[8] = $ 4,896/yea

(1) Fixed cost/year = $11,296.0

(2) Fixed cost/H = $ 8.6

Operating Cost (based on productive time)

Maintenance and repair:

(100% (see tabulation, page 8) × D) ÷ 1,300 = $ 4.92

- Fuel: (0.037 × 80 × .60) $ 1.78
- Lubricants:
  - Engine oil ((.0005 × 80) + (4/80)) × $2.00 = $.18
  - Other lubricants (50% of engine oil) = $.09
  - $.27

(3) Operating Cost per Productive Time = $ 6.97

Fixed and Operating Equipment Costs per Productive Time (excluding labor cost)

Fixed cost/H ($8.69) + Operating cost/H ($6.97) = $15.66

Labor Cost per Productive Time

($7.00/SH × $\frac{2000 \text{ SH})^{9}}{1300\text{H}}$ = $10.77

Fixed and Operating Equipment Costs per Productive Time with Labor Cost = $26.43

Example 11.— A contractor wishes to estimate the fixed and operating cost of a rubber-tired skidder costing $45,000 (F.O.B. factory price).

Preliminary Data and Determinations

- Description of equipment—diesel, 115 hp, 10 gallons of crankcase capacity, 120 hours between oil changes.
- Diesel fuel, $.60/gallon.
- Engine oil, $2.00/gallon.
- Interest 12%, insurance 3%, taxes 3%.
- Labor cost $7.00/hour (including the employer's contribution)
- Initial investment (P):

Purchase cost (without a grapple)	$45,000
Extra attachment cost (grapple)	$ 6,000
Sales taxes (4%)	$ 2,040
Freight cost (5 cents per pound) (shipping weight 15,000 lbs. × .05)	$ 750
Less tires cost	$–7,000
P =	$46,790

- Salvage value (S) (20% of P) $ 9,358
- Economic life (N) 3 yrs
- Scheduled operating time (SH) 2,000 hr/yr
- Utilization (see tabulation, page 3) 67%
- Productive time (2,000 × 67%)(H) 1,340 hr/yr.

Fixed Cost

- Depreciation (D) = (P−S)/N = ($46,790 − $9,358)/3 yr = $12,477.33/yr.
- Interest, insurance, and taxes (18% × AVI)[10] = .18 × $34,312.67 = $ 6,176.28/yr.

(1) Fixed cost per year = $18,653.61

(2) Fixed cost per Productive Time = $ 13.92

Operating Cost (based on productive time)

- Maintenance and repair: (60% (see tabulation, page 8) × D)/1,300 = $ 5.59
- Fuel: (0.037 × 115 hp × .60) = $ 2.55
- Lubricants:
  - Engine oil ((.0005 × 115) + (10/120)) × $2.00 = $ .28
  - Other lubricants (50% of engine oil) .14
  - = $ .42
- Tire ($7,000 × 1.15)/3,000 = $ 2.68

(3) Operating Cost Per Productive Time = $ 11.24

Fixed Operating Cost per Productive Time (excluding labor cost)

(2) + (3) = $13.92 + $11.24 = $25.16

Labor Cost per Productive Time

$7.00/SH × (2,000 SH/1,340 H) = $10.45

Fixed and Operating Cost of Equipment per Productive Time With Labor Cost = $35.61

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[8] *Average value of yearly investment (AVI)*

$$\text{AVI} = \frac{(P-S)(N+1)}{2N} + S = \frac{(40{,}000-8{,}000)(5+1)}{2(5)} + 8{,}000 = 27{,}270/\text{yr.}$$

[9] *$7.00/SH is based on the scheduled operating time. Operating cost in this example is based on productive time. Thus, multiplying $7.00/SH by 2000/1300, we can obtain the labor cost per productive time (H).*

[10] $$\text{AVI} = \frac{(P-S)(N+1)}{2N} + S = \frac{(46{,}790-9{,}358)(3+1)}{2(3)} + 9{,}358 = 34{,}312.67$$

RECOMMENDATION

Analyses and knowledge of fixed and operating cost of equipment significantly affect an owner's economic position and ability to stay in business. In the past, logging operations were incurred by low fixed cost (i.e., low investment on equipment) and high operating cost (i.e., high dependency on labor). Rapid mechanization has greatly increased fixed costs. Most logging is now capital intensive. This requires a continuous awareness of how to reduce equipment and operating costs and increase equipment productivity. Knowledge of all elements of equipment cost and how to determine them are paramount to successful logging.

To estimate cost of new equipment for which cost data are unavailable, industry data, manufacturer's guides or rules of thumb may be used initially. These estimates can later be refined as the owner's own cost data become available. There are so many variations in interest, insurance, taxes, fuel, lubricant, labor cost, etc., from one type of equipment to another and from one locality to another that no standard cost can be applied for estimating individual equipment cost. However, the owner can keep accurate cost data as a basis for estimation. These should be recorded daily by the operator, and reviewed by the logging supervisor, owner, or contractor at least weekly. Once the cost of equipment has been established with relative precision, it can be used as a standard. It can also provide an effective guide for improving the efficiency of logging operations and estimating production costs or logging operation cost.

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APPENDIX A

THE THEORY AND FORMULATION OF THE AVERAGE VALUE OF YEARLY INVESTMENT COST

Here we summarize the concept and theory for the average value of yearly investment cost $\left(AVI = \frac{(P-S)(N+1)}{2N} + S\right)$, and give reasons why this mathematical formula is usable only with the straight line method to calculate the depreciation.

Arithmetic Progression

An arithmetic progression is a sequence of numbers for which there is a constant d (the common difference) such that the difference between any two successive terms is equal to d (Lapedes, 1976).

The sequence 1, 3, 5, 7, 9 is an arithmetic progression having 5 terms, the first term is 1 and the common difference is +2. The sequence 9, 7, 5, 3, 1 is an arithmetic progression having 5 terms, the first term is 9 and the common differnce is −2.

If the first term and the common difference are given, the Nth term is obtained from the following formula:

$$PN = P1 + (N-1)\,d \qquad (1)$$

Where:

PN = the Nth term
P 1= the first term
d= the common difference.

To illustrate this equation, consider the preceding sequence (9, 7, 5, 3, 1).

The first term is 9 and the common difference is −2. Then, the 3rd and 4th terms can be obtained as follows:

$$P3 = 9 + (3-1)(-2) = 9 - 4 = 5$$
$$P4 = 9 + (4-1)(-2) = 9 - 6 = 3$$

We can find the sum of the first N terms of an arithmetic progression by using the following formula:

$$SN = \frac{N}{2}(P1 + PN) \qquad (2)$$

Where:

SN = the sum of the first + N terms
PI = the first term
PN = the Nth term

Substituting equation (1) for (2), the equation (2) can be written as follows:

$$SN = \frac{N}{2}(P1 + P1 + (N-1)\,d)$$
$$= \frac{N}{2}(2P1 + (N-1)\,d) \qquad (3)$$

If, as an example, we want to find the sum of the first 3 terms in sequence (9, 7, 5, 3, 1), then:

$$S3 = \frac{3}{2}(2(9) + (3-1)(-2))$$
$$= \frac{3}{2}(18-4)$$
$$= \frac{3}{2}(14)$$
$$= 21$$

The sum of the first 5 terms is:

$$S5 = \frac{5}{2}(2(9) + (5-1)(-2))$$
$$= \frac{5}{2}(18-8) = \frac{5}{2}(10)$$
$$= 25$$

Average value of yearly investment (AVI):

The tabulation for straight line method (page 4) can be written as follows:

$85,000; $71,400; $57,800; $44,200; $30,600; $17,000

This is a sequence and an arithmetic progression having 6 terms, the first term is $85,000 and the common difference is −13,600. It means we can use the equation (1) and (2) or (3) to find Nth term and the sum of the first Nth term. Here, the common difference of $13,600 is obtained by using the straight-line method; depreciation $= \frac{P-S}{N}$.

Thus, the equation (3) can be rewritten by substituting $-\frac{(P-S)}{N}$ for d and P for P1.

$$SN = \frac{N}{2}\left(2P + (N-1)\left(-\left(\frac{P-S}{N}\right)\right)\right)$$
$$= \frac{N}{2}\left(2P + \frac{P-PN-S+SN}{N}\right)$$
$$= \frac{N}{2}\left(\frac{2PN-PN+P-S+SN}{N}\right)$$
$$= \frac{PN+SN+P-S}{2}$$
$$= \frac{PN-SN+P-S+2SN}{2}$$
$$= \frac{P(N+1)-S(N+1)+2SN}{2}$$

Dividing this equation (the sum of the first N term) by Nth term, we can obtain the average value of this sequence (i.e. average value of yearly investment).

Average value of this sequence is:

$$\left[\frac{P(N+1) - S(N+1)+2SN}{2}\right] \div N$$

$$= \frac{P(N+1)-S(N+1)+2SN}{2N}$$

$$= \frac{(P-S)(N+1)}{2N} + \frac{2SN}{2N}$$

$$= \frac{(P-S)(N+1)}{2N} + S \qquad = AVI$$

Thus, the mathematical formula of AVI is based on the common difference (P−S)/N. For this reason, it can be used only as a straight-line method to calculate the depreciation.

The mathematical formula can be simplified, if salvage value is not to be taken into account, by substituting zero for S in this formula.

$$\text{AVI (no salvage value)} = \frac{(P-O)(N+1)}{2N} + O$$

$$= \frac{P(N+1)}{2N}$$

APPENDIX B

Machine Cost

Description and Data:

Manufacturer: ____________ Model: ____________ HP: ____________
Purchase price (f.o.b. delivered): $ ________
Less: tire cost ________
INITIAL INVESTMENT (P) $ ________
Salvage Value (S)(__ % of P) $ ________
Estimated Life (N) ______ years
Scheduled operating time (SH) ______ hrs/yr
Utilization (U) ______ %
Productive time (H) ______ hrs/yr
Average value of yearly investment (AVI) $ ______ /yr.
AVI = [((P−S)(N+1))/2N]+S

I. **Fixed Cost:**

Depreciation = (P−S)/N = $ ______ /yr.
Interest (__%), Insurance (__%), Taxes (__%)
Total__% × ($___/yr) = $ ______ /yr.
AVI
(1) Fixed cost per year $ ______
(2) Fixed cost per H (1 ÷ H) $ ______

II. **Operating Cost:** (based on productive time)
Maintenance and repair (__ % × ((P−S)/(N×H)) $ ______
Fuel (_____ gph × $____/gallon) $ ______
Oil & lubricants $ ______
Tires (1.15 × (tire cost)/tire life in hrs.) $ ______
(3) Operating Cost per H $ ______

III. **Machine Cost per H** *(without labor)* (2+3) $ ______

IV. **Labor Cost** *($* ____/hr ÷ U) $ ______

V. **Machine Cost per productive hr. with labor** (III. + IV) $ ______

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1980. Determining fixed and operating costs of logging equipment. U.S. Department of Agriculture Forest Service, General Technical Report NC-55, 16 p. U.S. Department of Agriculture Forest Service, North Central Forest Experiment Station, St. Paul, Minneosta.

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